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PROCEEDINGS

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THE PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON

THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

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Clerk of Publications . . . G. B. STRATTON, M.B.E.

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ZOOPLANKTON OF THE RIVER SOKOTO. THE ROTIFERA

By

J. GREEN

Bedford College, University of London

Accepted 12th April, 1960

(With 20 figures in the text)

Forty-one species of Rotifera are recorded from the River Sokoto, North Nigeria, and details of their seasonal abundance are given. There is a marked change in the composition of the rotifer fauna of the river when it floods in the single wet season. The cyclomorphosis of *Keratella tropica* begins with the appearance of the species in December. At this stage most individuals lack a left posterior spine. The left posterior spine then grows longer in successive samples until February or March and then decreases to very short lengths in June. The right posterior spine does not vary much throughout the cycle and is always positively correlated with the length of the lorica. The length of the left spine shows varying degrees of correlation with the length of the lorica according to the rate of change of length of the left spine. *Brachionus caudatus* shows synchronous changes of both its posterior spines, the lengths of which are positively correlated with the length of the lorica. The relation of these findings to the general theories of cyclomorphosis is discussed. The flotation theory of Wesenberg Lund is rejected from application to the species studied. The necessity of considering cyclomorphic phenomena in relation to body size is emphasized.

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INTRODUCTION

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INTRODUCTION

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Green (1960). The dominating feature of the hydrology is the flooding of the river during the single wet season (Fig. 1). This has great effects on the abundance and composition of the zooplankton.

Temperatures in the River Sokoto are generally high, but during December and January a cold wind, the harmattan, blows southwards from the Sahara, and cools the river (Fig. 1). The annual cycle in pH is also shown in this figure, the main feature is a marked lowering of pH when the river is in flood and more acid water is washed out from bordering swamps.

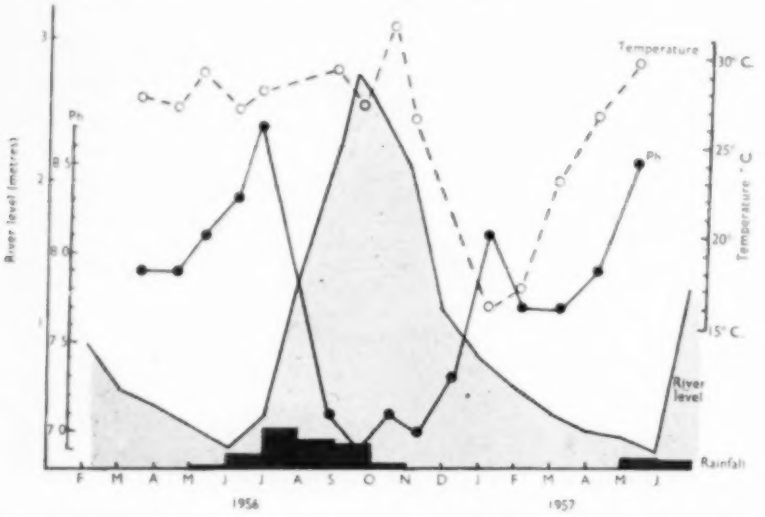

Fig. 1.—Some features of the environment. Temperature and pH are given for the pool Fesafari, the data for the river are very similar (*cf.* Holden & Green, 1960).

When the floods subside a pool called Fesafari becomes isolated from the main channel of the river. The seasonal changes in form of *Keratella tropica* and *Brachionus caudatus* have been followed in this pool in preference to the river because the populations in the pool were more likely to be homogeneous than the constantly changing populations swept down by the river.

The seasonal cycles of temperate zone rotifers are now well known (*cf.* Kofoid, 1908 ; Wesenberg Lund, 1930 ; Carlin, 1943), but very little is known of their cycles in tropical countries. The work described below, while imperfect in details, provides a general account of the seasonal cycle of rotifers in a tropical river.

METHODS

The plankton was collected by Mr Holden, using a fine meshed plankton net which was towed for a fixed distance just below the surface of the water. Details of the sampling stations in the main channel and in the pool Fesafari are shown on a map in Holden & Green (1960).

The samples were preserved in 5 per cent formalin, and were in excellent condition when I received them for study. The volume of each sample was made up to 30 ml. and sub samples were taken after mixing each sample thoroughly. All the animals in a sub-sample of 0·5 ml. were counted and assigned to major groups, such as Cladocera, Calanoida, Rotifera, etc. This gave a measure of the actual abundance of each group. The relative abundance of each species within the major groups was estimated by another series of samples in which 100 specimens of each group were identified to specific level.

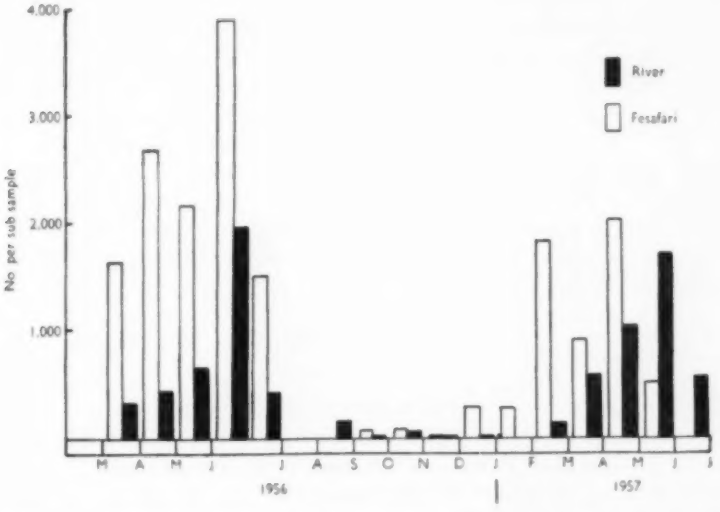

Fig. 2.—Seasonal variation in total rotifers in the River Sokoto and the pool Fesafari. Notice in this figure that two samples were taken in June 1956 but no sample was taken in July ; this also applies to the other diagrams showing seasonal occurrence. Dates of samples are given in Tables 1 and 2. Each sub sample represents the number of individuals in approximately one-third of a cubic metre.

The technique used for this series of counts varied slightly with the different groups. Rotifers were identified and counted after they had been mixed with a little lactic acid containing lignin pink. This stained the loricas of many of the species and the refractive index of lactic acid is such that the sculpturing of the lorica was easy to see. Preparations made in this way were examined on a specially ruled glass slide with lines at intervals just a little under the field diameter of a monocular microscope with a 16 mm. objective. The slide was moved with a mechanical stage and each row was systematically searched for rotifers. The sequence in which rotifers were encountered was essentially random, and the counts can be regarded as reasonable estimates of the relative abundance of each species.

A parfocal higher powered objective was used to identify any small or difficult specimens which were not recognizable under the lower power.

The figures showing seasonal occurrence were drawn using data calculated from the relative abundance of each species and the total rotifers in each sub sample.

SYSTEMATIC SURVEY AND SEASONAL OCCURRENCE

Order BDELLOIDEA

Many of the species belonging to this group are not identifiable in preserved material. Several specimens were found in samples from the river taken between July and December, which appeared to belong to the genus *Habrotrocha*. These would not be true planktonic species, and their occurrence in the samples is related to the flooding of the river.

One species of this order was identifiable as follows.

Family PHILODINIDAE

Rotaria neptunia Ehrenberg

A few specimens were found in samples taken from the river on September 12th, 1956, and April 6th, 1957. Most of the species in this genus are bottom dwellers, but the present species has been recorded in the plankton by other authors, for instance Kofoid (1908) in the River Illinois, and Beauchamp (1932) in the East African Lakes.

Order MONOGONONTA

Sub-order *PLOIMA*

Family BRACHIONIDAE

This family is by far the best represented of all the rotifer families in the samples ; no less than twenty of the species are brachionids. The relative importance of the members of this family can be seen in Tables 1 and 2.

The taxonomy of this family is complex, particularly within the genera *Brachionus* and *Keratella*. Both these genera were revised by Ahlstrom (1940, 1943), but since these revisions there have been additions, and changes in the status of various forms have been proposed (Gillard, 1948 ; Hauer, 1953, 1957 ; Carlin, 1943 ; Berzins, 1954, 1955).

Anuraeopsis navicula Rousselet (Fig. 3 a)

The specimens from the Sokoto were about 93 μ long and 46 μ wide, and they agree with the form described from Lake Nakavali by Beauchamp (1932) as the variety *coelata*. Gillard (1948) believes that this may prove to be a geographical race, and places *A. punctata* Evens (1947) as a synonym of Beauchamp's variety.

This species was not found in the main channel of the river, but was found in small numbers in Fesafari in April and June.

Brachionus bennini (Leissling) (Fig. 3 f)

A single specimen was found in the sample taken from the river on March 4th, 1957. It has not previously been recorded in West Africa, but it has been found in East Africa.

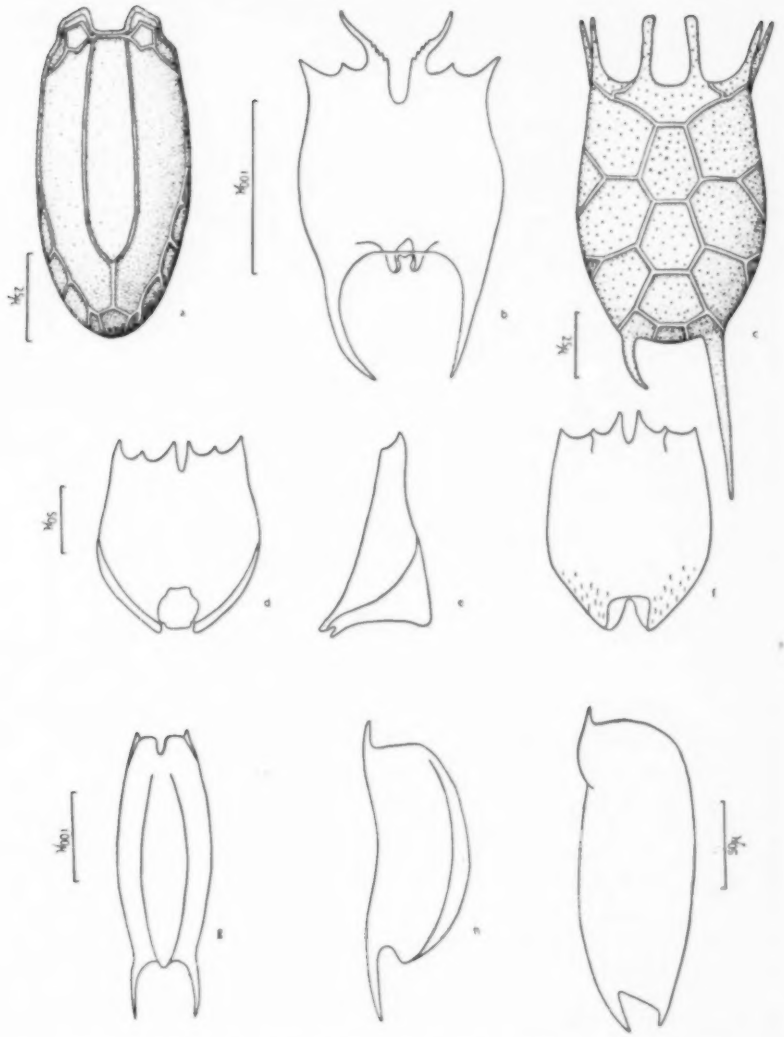

Fig. 3.—Brachionidae from the River Sokoto and the pool Fesafari. a, *Anuraeopsis navicula*, dorsal view. b, *Brachionus quadridentatus*, dorsal view. c, *Keratella tropica*, dorsal view. d, *Brachionus bidentatus*, dorsal view. e, *B. bidentatus*, lateral view. f, *Brachionus bennini*, dorsal view. g, *Mytilina ventralis*, dorsal view. h, *M. ventralis*, lateral view. i, *M. ventralis* f. *brevispina*, lateral view. Note that i is drawn to twice the scale of g and h.

Brachionus bidentata Anderson (Fig. 3 d, e)

A single specimen was found in the sample taken from the river on June 10th, 1957. I have not seen any previous records of this species in Africa.

TABLE 1

Family Brachionidae. Relative numbers of each species in the River Sokoto, as percentage of the total rotifers in each sample.

	14 Mar	10 Apr	5 May	6 Jun	26 Jun	14 Aug	12 Sep	9 Oct	7 Nov	1 Dec	1 Feb	4 Mar	6 Apr	16 May	10 Jun
Brachionus															
bennini	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
bidentata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
budapestinensis	–	3	3	–	1	–	–	–	–	–	–	–	–	4	–
calyciflorus	+	14	3	4	4	1	–	–	1	4	1	5	3	+	1
caudatus	78	40	42	32	27	6	10	2	7	26	58	73	55	32	12
diversicornis	–	1	4	–	–	–	–	–	2	–	–	–	2	1	–
falcatus	2	6	11	5	15	1	–	12	4	6	2	3	5	10	4
quadridentatus	4	1	1	–	–	4	2	4	–	–	3	1	1	–	8
Dipleuchlanis															
propatula	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–
Euchlanis															
triquetra	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Epiphanes															
macroura	–	–	–	+	–	–	–	–	–	–	–	–	–	+	–
Keratella															
tropica	1	–	1	–	1	1	–	–	–	2	32	14	3	–	5
Macrochaetus															
collinsi	–	–	–	–	–	8	2	2	8	6	–	–	–	–	–
Mytilina															
ventralis	–	–	–	–	–	1	–	–	1	2	–	–	–	–	–
Notholca															
acuminata	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Platyias															
patula	12	5	–	–	–	11	–	–	–	–	–	1	1	–	5
quadricornis	+	3	–	–	–	6	1	–	–	4	–	–	–	–	6
Trichotria															
tetractis	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–

+ indicates present, but less than 1 per cent of total rotifers.

TABLE 2

Family Brachionidae. Relative numbers of each species in Fesafari, as percentage of the total rotifers in each sample.

	23 Mar	18 Apr	7 May	7 Jun	25 Jun	19 Sep	13 Oct	10 Nov	8 Dec	8 Jan	3 Feb	7 Mar	5 Apr	17 May
Anuraeopsis														
navicula	–	2	–	–	+	–	–	–	–	–	–	–	–	–
Brachionus														
calcyciflorus	1	1	2	–	3	–	–	–	+	–	–	1	–	1
caudatus	35	66	77	47	66	6	4	18	9	21	75	69	61	10
falcatus	20	6	15	9	7	–	2	12	5	13	5	16	26	25
quadridentatus	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Dipleuchlanis														
propatula	–	–	–	–	–	–	7	–	–	–	–	–	–	–
Diplois														
davidsiae	–	–	–	–	–	12	10	–	–	–	–	–	–	–
Euchlanis														
dilatata	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Keratella														
tropica	8	4	5	+	–	–	–	–	3	60	20	14	10	–
Macrochaetus														
collinsi	–	–	–	–	–	–	1	3	–	–	–	–	–	–
Mytilina														
ventralis	–	–	–	–	–	1	1	–	–	–	–	–	–	–
Platyias														
patula	–	–	–	–	–	1	–	–	6	–	–	–	–	–
quadricornis	–	–	–	–	–	5	1	3	–	–	–	–	–	1

+ indicates present, but less than 1 per cent of total rotifers.

Brachionus budapestinensis Daday

This species was present in small numbers in the river in April and May 1956, and a single specimen was found in June of the same year. Small numbers again appeared in the river in May 1957. It was not found in the pool Fesafari. Kofoid (1908) found this species in the River Illinois from the end of June until the early part of October, and regarded this as a mid-summer planktont, with its maximum near the maximum summer temperature.

Brachionus calyciflorus Pallas

The seasonal occurrence of this cosmopolitan species is shown in Fig. 4. It was generally more abundant in the main channel than in Fesafari.

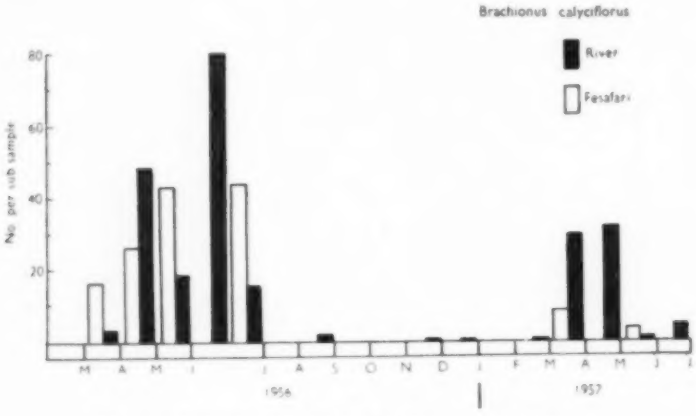

Fig. 4.—Seasonal occurrence of *Brachionus calyciflorus*.

Brachionus caudatus Barrois & Daday (Fig. 6)

This is the dominant rotifer in the river. The seasonal occurrence is shown in Fig. 5. The cyclomorphosis of the species is dealt with on pages 516-519.

Some workers regard this species as a mere variety of *B. angularis* ; Kofoid (1908) goes so far as to say that he does not regard it as worthy of even varietal distinction. Fig. 6 shows that in the Sokoto a whole series exists, from forms with very long spines to much smaller forms, which, although mature and carrying eggs, lack any clearly developed spines. I have retained the name *B. caudatus* because I believe that the small specimens from the Sokoto are by no means the same as *B. angularis*, which is typically a much larger form lacking any trace of posterior spines. Gillard (1948), Hauer (1953, 1957) and Voigt (1957) all retain *B. caudatus* as a distinct species.

All the specimens from the Sokoto had only two spines on the anterior border of the lorica. It is of interest that in North-East Brazil Hauer (1953) found a series of forms of *B. caudatus* showing the same variation in the posterior spines as that found in the Sokoto, but all having six spines on the anterior border of the lorica.

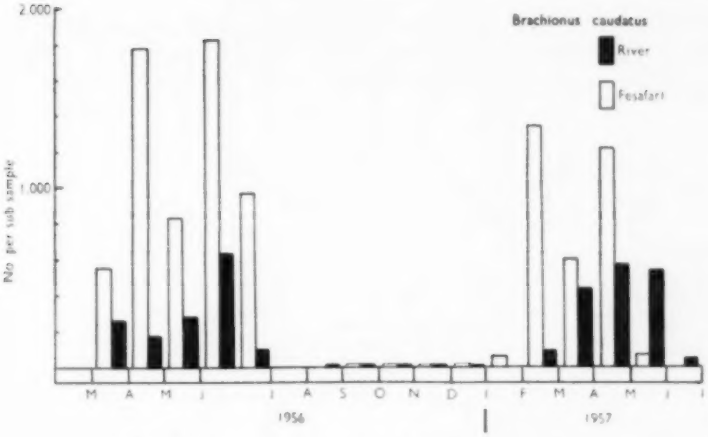

Fig. 5.—Seasonal occurrence of *Brachionus caudatus*.

Brachionus diversicornis (Daday)

This species has long been known under the name *Schizocerca diversicornis*, but most recent authors agree that it should be placed in the genus *Brachionus*. In Europe it is generally regarded as a summer form. It has been recorded from the summer plankton of the Rhine (Lauterborn, 1898) and the Elbe (Schorler, 1900). It occurred in the River Sokoto in April and May in 1955, 1956 and 1957. A few specimens were also found in November 1956, indicating that the species might have a second pulse when conditions are suitable. No specimens were found in the samples from Fesafari.

A specimen from the sample taken on April 6th, 1957, was found to be infected with *Dimoerium hyalinum* Przesmycki, a parasite of uncertain systematic position. The form in *B. diversicornis* consisted of numerous oval bodies measuring $32 \times 14\,\mu$.

Brachionus falcatus Zacharias

This species is only found where the water is warm ; in Europe it is a summer form, and it is widespread in the tropics. The seasonal occurrence is shown in Fig. 7. This species was always more abundant in the pool Fesafari than in the main channel. In Fesafari it sometimes formed as much as 45 per cent of the total rotifers.

Although no detailed measurements have been made there does not seem to be much seasonal variation in the length of the posterior spines of this species in the Sokoto. The variation in spine length in a single sample is illustrated in Fig. 8.

In the sample taken from Fesafari on December 8th, 1956, a newly-hatched specimen was found. The long anterior spines were still curved ventrally around the lorica which was distinctly rounded and egg-shaped. The length of the lorica was $98\,\mu$ and the posterior spines were $72\,\mu$ long. When these dimensions are compared with those of the largest adults from the same

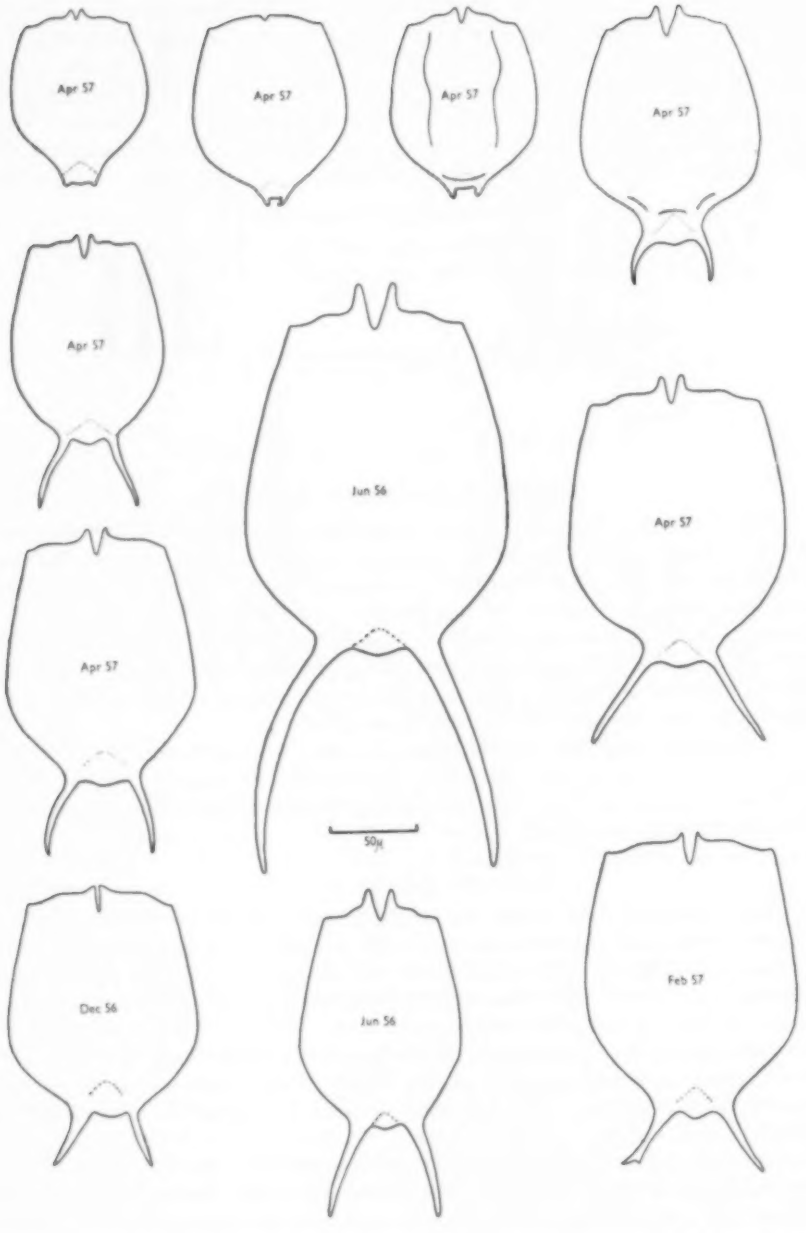

Fig. 6.—Variation in the form of *Brachionus caudatus*. All the specimens were taken from Fesafari and all are drawn to the same scale.

locality (lorica length 144 μ, posterior spine length 170 μ) they indicate that the posterior spine grows allometrically ; the lorica does not double its hatching length, while the posterior spines become more than twice as long as they were at hatching.

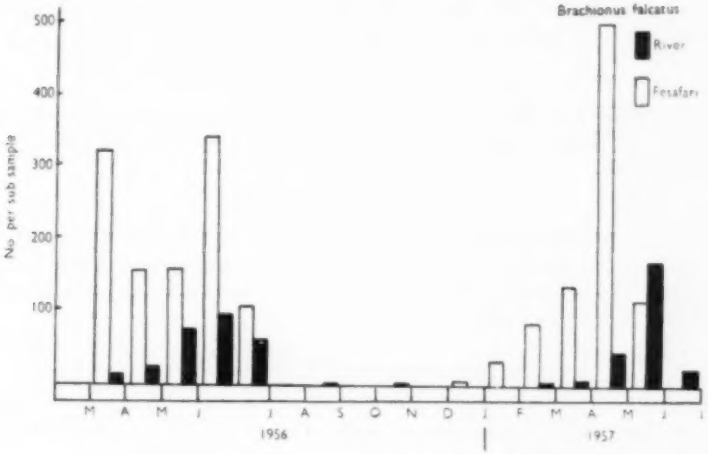

Fig. 7.—Seasonal occurrence of *Brachionus falcatus*.

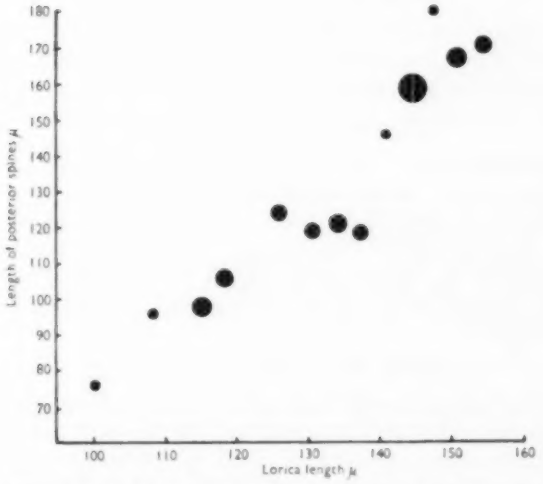

Fig. 8.—Relation between lorica length and posterior spine length in a sample of fifty *Brachionus falcatus* taken from Fesafari, 7th June 1956. The diameter of each dot is proportional to the number of animals on which it is based ; the largest represents fifteen and the smallest a single specimen.

Brachionus quadridentatus Hermann

A single specimen was found in the sample from Fesafari on September 19th, 1956. It was a remarkably fine specimen (Fig. 3 b) with long diverging anterior median spines with the middle thirds of their inner borders serrated. Specimens with less well developed spines were found in the main channel irregularly throughout the year. This is a cosmopolitan species regarded as a summer form in temperate climates.

Dipleuchlanis propatula (Gosse)

Small numbers of this species were found in the river in August, and it was somewhat more numerous (7 per cent of the total rotifers) in Fesafari in October.

Diplois daviesiae Gosse

No specimens were found in the main channel of the river, but there was a small outburst in Fesafari in September and October, when it formed up to 12 per cent of the total rotifers. It does not seem to have been recorded previously from West Africa.

Epiphanes macroura Barrois & Daday

Specimens from the Sokoto agree with the figures given by Beauchamp (1932) of East African specimens under the name *Notops mollis* Hempel, which is a synonym of *E. macroura*.

This species was present in small numbers in the river in June 1956 and May 1957. It was not found in Fesafari.

Euchlanis dilatata Ehrenberg

A single specimen was found in the sample from Fesafari on November 10th, 1956. This species has been recorded from Gambia (Berzins, 1957) and from the Belgian Congo (Evens, 1959).

Euchlanis triquetra Ehrenberg

A single specimen was found in the sample from the river on August 14th, 1956. This species was recorded as fairly common in the swamps south of Bolgatanga, Ghana, by Russell (1956) and a single specimen has been recorded from Gambia Berzins, 1957). The record by Russell is open to some doubt because he mentions a ventral plate, which is absent in the true *triquetra* Ehrenberg, but present in *E. incisa* Carlin which has been confused in the past with *E. triquetra*.

Keratella tropica (Apstein) (Fig. 3 c)

The synonymy of this species has recently been given in detail by Berzins (1955). It has frequently been regarded as a variety of *K. valga* (Ehrenberg), but it can be distinguished from that species by the sculpturing of the lorica. *Keratella valga* has three hexagons on the dorsal surface ; the last hexagon has the posterior border of the lorica as one of its sides. In *K. tropica* the dorsal surface has three hexagons and a small four-sided figure between the posterior border of the lorica and the last hexagon (Fig. 3 c). The two species differ

in their geographical distribution ; *K. valga* is predominantly found in Europe, with some records from temperate Asia ; *K. tropica* is found in the South-West of North America, South America, Africa, from Egypt to the Cape, but it has not previously been found in West Africa. There are also records from Madagascar, Ceylon, India, Indonesia, New Zealand, China, Japan, and the southern parts of the Soviet Union around the Caspian Sea.

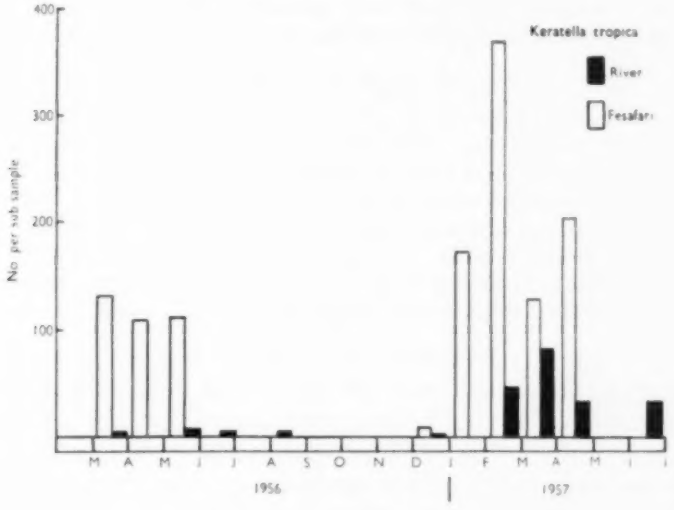

Fig. 9.—Seasonal occurrence of *Keratella tropica*.

The seasonal occurrence of this species is shown in Fig. 9. The numbers are generally much higher in Fesafari than in the main channel, but while the species disappears from the pool by the end of June it can still be found in the river as late as August.

Macrochaetus collinsi (Gosse)

This is a species characteristic of the flood waters. It appeared in the river in August and persisted until December, forming up to 8 per cent of the total rotifers. The numbers appearing in Fesafari were much smaller, and the seasonal occurrence was limited to October and November.

Mytilina ventralis (Ehrenberg)

Small numbers of this species were found when the river was in flood. The duration of occurrence in the river extended from August to December, but only from September to October in Fesafari.

Two distinct morphological forms were found : one (Fig. 3 i) corresponds with the form *brevispina* Ehrenberg, the other is similar to the var. *macracantha* (Gosse) but differs in that the median posterior part of the lorica is not extended into a spine (Figs. 3 g & h).

Notholca acuminata (Ehrenberg)

Three specimens were found in the sample from the river on May 5th, 1956. I have not seen any previous record of this species from Africa.

Platyias patulus (O. F. Muller)

This species appeared regularly in small numbers in the river from March to May in 1955, 1956 and 1957. It was also found in August 1956 and June 1957. In Fesafari it was found very sparsely in September and December 1956, presumably being washed into the pool by the flooding river.

Platyias quadricornis (Ehrenberg)

The occurrence of this species in the river paralleled that of *P. patulus* to a marked extent, the only difference of any note was the occurrence of *P. quadricornis* in the main channel in December 1956. In Fesafari this species was only found in small numbers from September to November 1956; again like *P. patulus* it was probably washed into the pool by the flooding river.

Both species of *Platyias* may be regarded as only partly planktonic, because they spend much of their time among water plants. Both species have widespread distributions and may be cosmopolitan.

Trichotria tetractis (Ehrenberg)

A single specimen was found in the sample from the river on August 14th, 1956.

Family LECANIDAE

Only one genus of this family is represented in the samples from the Sokoto, but this genus, *Lecane*, is the most abundant of all the rotifers during the wet season. The numbers per unit volume of water are low, but over half the rotifers found in the plankton during the wet season belong to this genus.

TABLE 3

Genus *Lecane*. Relative numbers of each species, as a percentage of the total number of rotifers. The first figures under each date refer to the main channel of the river and the figures in brackets refer to Fesafari. Only data for 1956 are given, because these include all the occurrences of the species apart from one record of *L. bulla* which formed 1 per cent of the total rotifers in the river in June 1957 (see Fig. 11).

	May	Jun	Aug	Sep	Oct	Nov	Dec
Lecane bulla	– –	– –	1 –	10 (51)	26 (23)	24 (27)	12 –
Lecane curvicornis	– –	– –	– –	– (3)	– (9)	4 –	2 –
Lecane hornemanni	– –	– –	– –	– –	– –	– (1)	– –
Lecane leontina	– –	– –	12 –	10 (8)	12 (11)	16 –	2 –
Lecane luna	– –	– –	17 –	4 (3)	18 (11)	– –	– –
Lecane quadridentata	– –	– –	– –	– –	– –	2 –	4 –
Lecane ungulata	1 –	1 –	2 –	– (2)	– (4)	6 –	– –

Lecane bulla (Gosse) (Fig. 10 d)

The appearance of this species in the plankton is associated with the floods which wash out rotifers from the bordering backwaters of the river. This is the most abundant of all the rotifers when the river level rises. Jennings (1900) noted that this was probably the most abundant species of its genus

in richly vegetated backwaters. This is a cosmopolitan species, but the only previous record of its occurrence in West Africa is that of Berzins (1957) from Gambia.

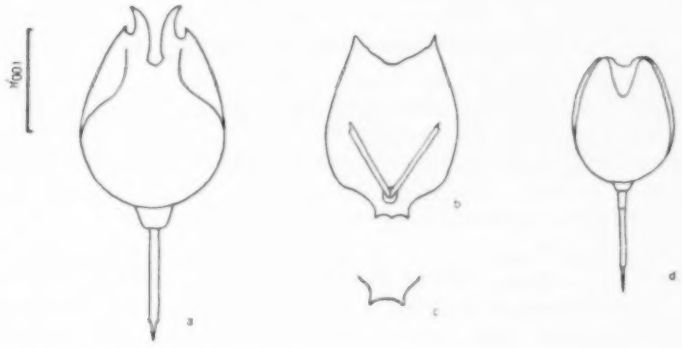

Fig. 10.—*Lecane* spp. from the River Sokoto, December 1956. a, *L. quadridentata*. b and c, *L. leontina*. d, *L. bulla*. All are drawn to the same scale.

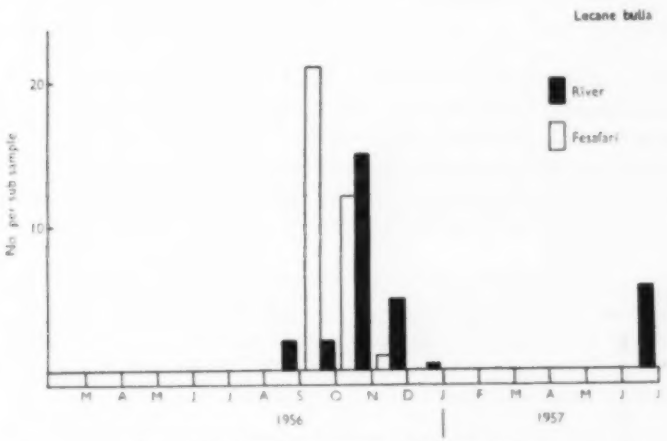

Fig. 11.—Seasonal occurrence of *Lecane bulla*.

The seasonal occurrence of *L. bulla* is shown in Fig. 11 ; it forms a marked contrast with the other seasonal distributions which have been figured.

Lecane curvicornis (Murray)

The specimens from the Sokoto agree in detail with the figures and description given by Hauer (1937/8) of a specimen from Sumatra. The species has also been found in North, Central and South America, Central Africa and Europe. Berzins (1957) records it from Gambia and Russell (1956) records it from Ghana.

In Fesafari this species was found in September and October 1956, and formed up to 9 per cent of the total rotifer population. It appeared somewhat later in the main river channel, being found only in November and December 1956, and never forming more than about 4 per cent of the total rotifers.

Lecane hornemanni (Ehrenberg)

Only a single specimen was found. This occurred in the sample taken from Fesafari on November 10th, 1956. This species does not seem to have been recorded previously from Africa.

Hauer (1937/8) gives the lorica length as ranging from 84–110 μ, and the toe length as 30–35 μ. The specimen from Fesafari had a lorica length of 101 μ, and the toes were 36 μ long.

Lecane leontina (Turner)

This is a cosmotropical species which has been recorded in West Africa from Ghana (Russell, 1956) and Gambia (Berzins, 1957). The Sokoto specimens included forms with a small median posterior spine (Fig. 10 b).

This species was found in the river from August to December, forming up to 16 per cent of the total rotifers. In Fesafari the seasonal occurrence was more restricted ; September and October were the only months in which it was found.

Lecane luna (O. F. Müller)

A cosmopolitan species which has been recorded from Ghana (Russell, 1956) and Gambia (Berzins, 1957).

This species was found in the river (August) before it was found in Fesafari (September) and it persisted in both localities until October, forming up to 18 per cent of the total rotifers in the river.

Lecane quadridentata (Ehrenberg) (Fig. 10 a)

This species has not previously been recorded in West Africa, and it is not included in the list of Belgian Congo species by Evens (1949). It was found sparingly in samples from the river in November and December, but was not found in samples from Fesafari.

Lecane ungulata (Gosse)

This cosmopolitan species occurred irregularly in samples from the river, occasional specimens being found in May, June, August, and somewhat higher numbers in November. In Fesafari the seasonal occurrence was restricted to September and October.

Family NOTOMMATIDAE

Scaridium longicaudum (O. F. Muller)

This widespread species usually lives among plants. It was found in small numbers in the river in December 1956, but was not found in the samples from Fesafari.

Family TRICHOCERCIDAE

Trichocerca bicristata (Gosse)

This species is generally found among plants and detritus, but it has also been found as a regular member of the plankton, for instance by Kofoid (1908) in the River Illinois. It has not previously been recorded in West Africa.

In the River Sokoto it was present from September to December, and formed up to 14 per cent of the total rotifers. It was less abundant in Fesafari and the duration of occurrence did not extend beyond November.

Trichocerca longiseta (Schrank)

A single specimen was found in the sample taken from Fesafari on April 6th, 1954. This species was recorded as rare in the swamps near Bolgatanga, Ghana, by Russell (1956), but was not recorded from Gambia by Berzins (1957).

Family ASPLANCHNIDAE

Asplanchna brightwelli Gosse

The seasonal occurrence of this species is shown in Fig. 12. The species is most abundant from April to June, with sporadic appearances at other times. The relative number in relation to other rotifers (i.e. as a percentage of the total rotifers) is much higher in the river than in Fesafari, and in 1957 it failed to appear in Fesafari. This may be a factor of some importance for the other rotifers because members of the genus *Asplanchna* are well known as predators of rotifers. In the sample taken from Fesafari on June 7th, 1956, several *A. brightwelli* were found with *Anuraeopsis navicula* in their stomachs.

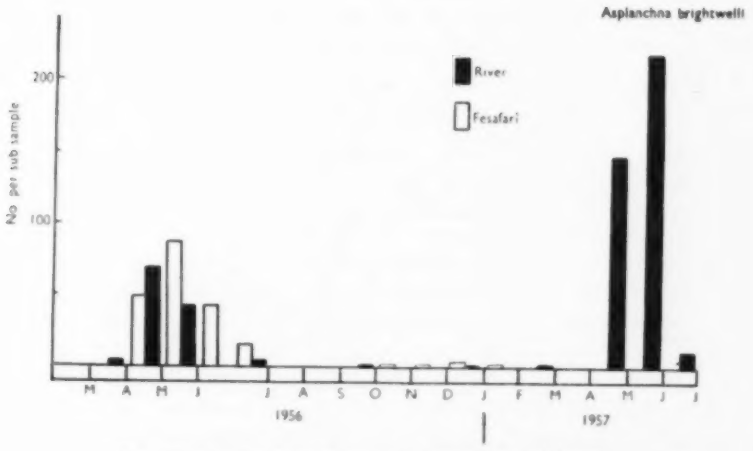

Fig. 12.—Seasonal occurrence of *Asplanchna brightwelli*.

Family SYNCHAETIDAE

Synchaeta sp.

There was an outburst of an unidentifiable *Synchaeta* species in Fesafari in December 1956. No specimens were found in the river, but in Fesafari this rotifer formed over 70 per cent of the total rotifers in the December sample. A few specimens were still present in the January sample, but none were found at any other time of year.

Polyarthra sp.

A single specimen of a *Polyarthra* species was found in the December 1956 sample from Fesafari. The body was about 100 μ long and 79 μ wide. The lateral spines were 108 μ long and 13 μ wide ; ventral spines, about 40 μ long, were present. The specimen is clearly allied to *P. dolichoptera* (Idelson) as redescribed by Carlin (1943), but I have hesitated to asign it definitely to this species because it was not particularly well preserved.

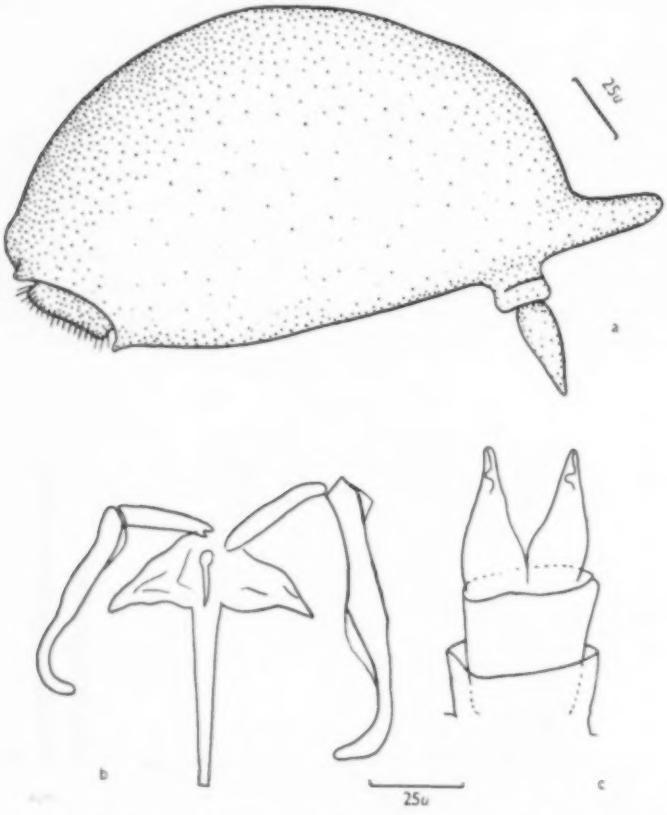

Fig. 13.—*Pseudoploesoma* sp. a, lateral view of uncleared specimen. b, ventral view of jaws cleared in sodium hydroxide. c, foot of cleared specimen, slightly squashed.

Pseudoploesoma sp. (Fig. 13)

A single specimen was found in the sample from Fesafari on November 10th, 1956. The body was 216 μ long, and the toes 36 μ long. These are close to the dimensions given for *P. formosum* Myers, but I have not assigned the specimen to this species because no fossettes were found on the lorica. Since *Pseudoploesoma* is known only from North America it was decided to examine the jaws of the Sokoto specimen to compare with the original description. The specimen was cautiously cleared with a solution of sodium hydroxide. This gave further details of the structure of the foot (Fig. 13 c) and showed that the jaws were virgate in form, agreeing in general with those figured by Myers (1934), but showing some differences in detail (Fig. 13 b). Treatment with sodium hydroxide also revealed the parabuccal processes, so that assignment to the genus *Pseudoploesoma* is justified. The lack of fossettes on the lorica, and the detailed differences in the jaws indicate that this specimen is distinct from *P. formosum*, but I do not feel justified in basing a new species on a single specimen which required drastic treatment to reveal its generic characters.

Sub-order *FLOSCULARIACEA*

Family TESTUDINELLIDAE

Testudinella patina

This cosmopolitan species occurred somewhat erratically in the samples, being most frequently found in the river during the wet season, but occurring in small numbers throughout the year. It was very scarce in Fesafari ; single specimens were found in January, April and October.

Filinia longiseta (Ehrenberg)

Small numbers were found in the river between May and September 1956, the only occurrence in 1957 was in April when it formed about 6 per cent of the total rotifers. Only single specimens were found in Fesafari in March and June 1956. This species is known from river plankton in Europe, North America and Manchuria.

Filinia sp.

Single specimens were found in Fesafari on the 7th and 25th June, 1956. The specimens had oval bodies, 108 μ long ; the terminal spine was 288 μ long, and the lateral spines varied between 268 and 342 μ. They run down to *F. maior* Colditz in Voigt (1957), but the spines are much shorter than the dimensions given by that author and by Carlin (1943). A further cause for doubt is the occurrence of *maior* as a winter form in Europe, whereas the specimens from the Sokoto were collected during the hottest season.

Tetramastix opoliensis Zacharias

The seasonal occurrence of this species is shown in Fig. 14. It is a summer form in Europe, and is widespread in the tropics. There are several records of its occurrence in flowing waters.

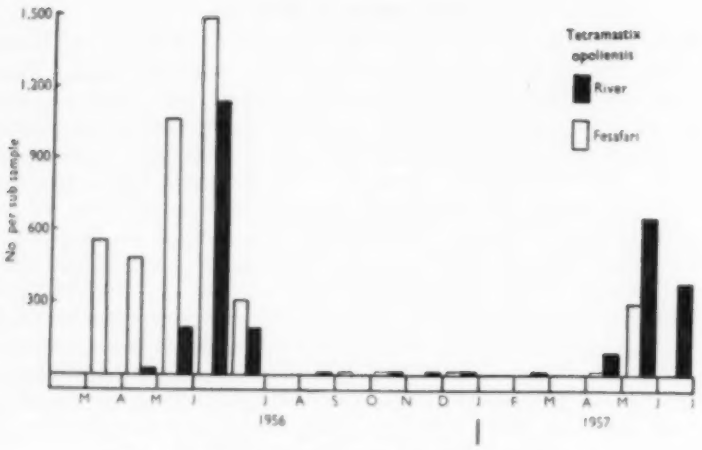

Fig. 14.—Seasonal occurrence of *Tetramastix opoliensis*.

Sub-order *COLLOTHECACEA*

Family COLLOTHECIDAE

Collotheca pelagica (Rousselet)

This is a planktonic representative of a group which is mainly sessile. Only a single specimen was found in the river in November 1956.

SEASONAL VARIATION IN NUMBER OF SPECIES

The total number of species observed in this study is forty-one ; samples from the river yielded thirty-one species, twenty of which were also found in the pool Fesafari. The samples from Fesafari yielded thirty species, of which ten were not found in the main channel. The two stations thus had roughly the same number of species and two-thirds of these they had in common.

Many of the species which were not shared by the two stations were rare, and were found only once or twice in the samples, but some showed a well-marked development of their population at one station while remaining absent from the other. The most striking example is the *Synchaeta* species which formed over 70 per cent of the total rotifers in Fesafari in December 1956 and yet was not found in the December sample from the river.

When the numbers of species in each monthly sample are considered it is seen that there is a marked increase when the river is in flood (*cf.* Table 4 and Fig. 1). This increase in the number of species occurs in spite of a great decrease in the total number of specimens (*cf.* Fig. 2). This is an unusual state of affairs. The general rule is that when conditions are favourable for animals then the number of species is high ; when conditions are unfavourable or extreme the number of species falls although the total number of individuals may be very large (*cf.* Hesse, Allee & Schmidt, 1937, p. 30). Conditions in the River Sokoto during the floods are unfavourable for plankton production

TABLE 4

Seasonal variation in the number of species present in a sample of 100 individuals.

Month	Number of species in main channel	Number of species in Fesafari	Total number of species in both samples
March	10	6	12
April	11	7	13
May	12	6	12
June	10	7	11
July	no sample	no sample	—
August	17	no sample	—
September	13	13	18
October	9	16	17
November	15	11	20
December	16	9	19
January	no sample	6	—
February	7	3	7
March	8	4	8
April	11	5	11
May	8	5	9
June	11	no sample	—

(Holden & Green, 1960), and yet we have an increase in the number of rotifer species. This increase is due to species which normally dwell among the vegetation of the bordering swamps being washed into the river. Many of the species occurring in the plankton samples during the floods are not true plankton species.

A consistent feature of the occurrence of the flood water species is the shorter period in which they may be found in Fesafari compared with the main channel of the river. This is due to the isolation of the pool causing a lag before the rising river reaches it, washing the vegetation dwellers into the plankton of the pool. The earlier reduction in the rate of flow through the pool allows the vegetation dwelling species to settle down again earlier than they do in the river.

The effect of rate of flow on the number of species is seen when the numbers of species at any one time in the river and in Fesafari are compared (Table 4). The number of species at the two stations is similar during the floods, but once the water level falls a consistently higher number of species is found in the river. Although the number of species is generally higher in the river at any one time, the number of species found in the two stations during the whole period of sampling is roughly the same.

Seasonal changes in the composition of the rotifer population are further emphasized when the relative importance of each species is considered. Two quite distinct assemblages can be distinguished. The flood assemblage is dominated by the *Lecane* species (Table 3 and Fig. 11), with additional regularly occurring species such as *Macrochaetus collinsi* and *Trichocerca bicristata*. At other times the brachionids are the dominant group (Tables 1 and 2), with *Tetramastix opoliensis* (Fig. 14) as an important auxiliary.

CYCLOMORPHOSIS

Seasonal changes in the body shape of successive generations have been described in a number of temperate zone rotifers (Lauterborn, 1900, 1903 ; Krätzschmar, 1908, 1913 ; Wesenberg-Lund, 1908, 1930 ; Hartmann, 1918 ; Carlin, 1943 ; Ruttner-Kolisko, 1949 ; Gallagher, 1957), but there is as yet no convincing explanation of the phenomenon. Indeed, some of the accounts are inadequate even from a descriptive point of view. When the cyclomorphosis of tropical rotifers is considered there does not seem to be any detailed information available.

Two of the species from the Sokoto showed marked seasonal variation in the length of their posterior spines. A detailed numerical study has been made of this variation to find in what respects the tropical species resemble the temperate zone species and to see if they throw any light on the mechanisms underlying cyclomorphosis.

Keratella tropica

This species was studied by measuring 50 individuals from each sample in which it was present. The points used in making the measurements are shown in Fig. 15 b.

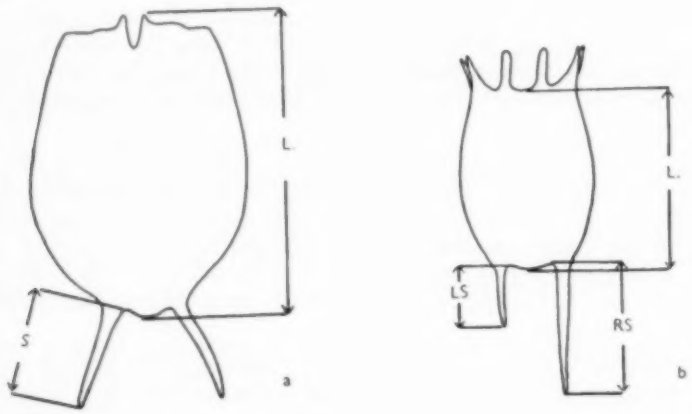

Fig. 15.—Diagram to show the measurements made on : a, *Brachionus caudatus* ; b, *Keratella tropica*. L—length of lorica ; LS—left posterior spine ; RS—right posterior spine ; S—posterior spine.

The data for 1954 extend from February 24th to April 6th ; no sample was available after the latter date. Samples were taken at weekly intervals during this period, so that they give a more detailed picture of part of the cycle which was studied at monthly intervals in later years. Fig. 16 shows that there was a steady increase in the length of the left posterior spine throughout this period, with only small changes in the length of the right posterior spine.

In a single sample taken in January 1955 none of the specimens had left posterior spines.

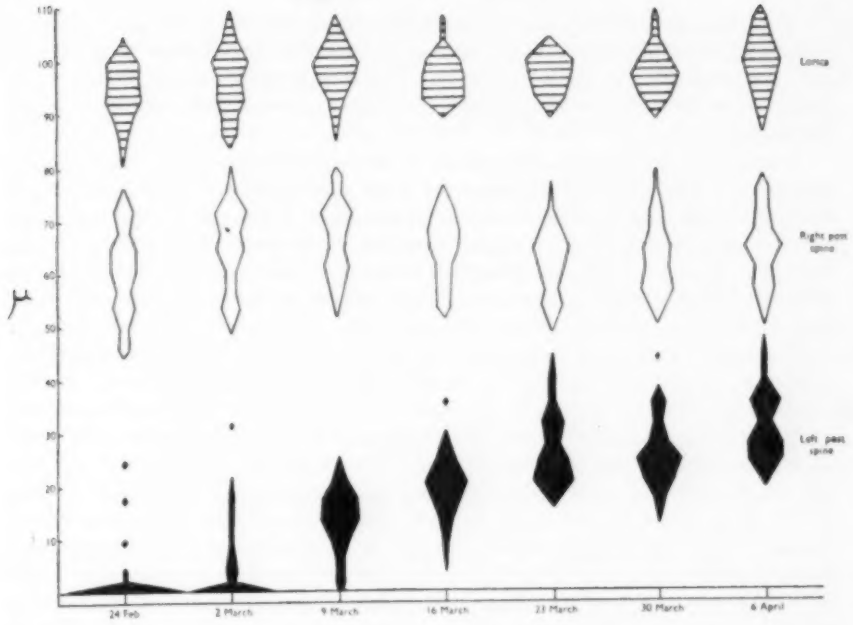

Fig. 16.—*Keratella tropica* : frequency distribution showing variation in dimensions in 1954.

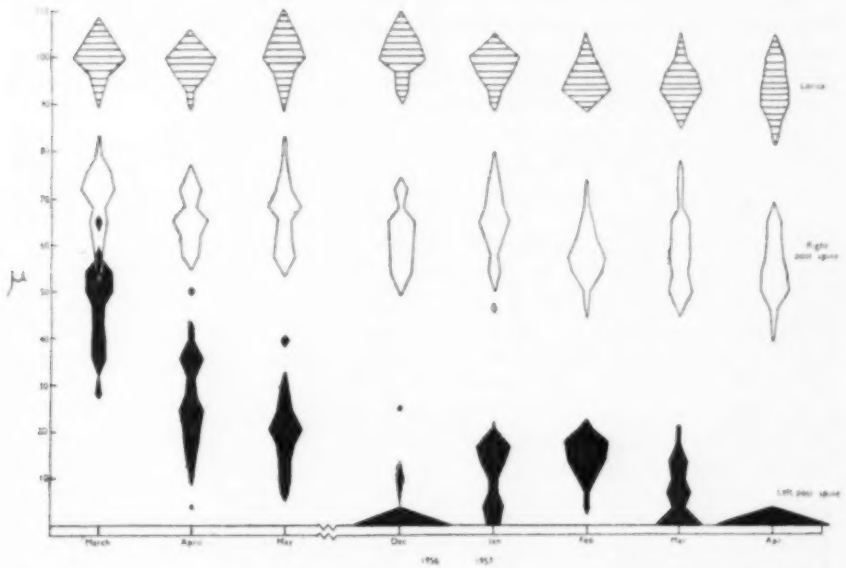

Fig. 17.—*Keratella tropica* : frequency distribution showing variation in dimensions during 1956 and 1957.

For 1956 samples taken at approximately monthly intervals are available from March to December. The species was present in the first sample, and had long left posterior spines (Fig .17). The length of the left spine decreased during April and May, and the species had disappeared from the samples by the end of June.

A reappearance, with a very short or no left posterior spine, was made in December. During the early part of 1957 a complete cycle was observed (Fig. 17). The length of the left spine increased until February then decreased to a very short length in April, and the species was absent from the May sample. The early decrease in length of the left spine and disappearance of the species in 1957 compared with other years is correlated with the rains beginning very early in 1957 ; the river in June 1957 was three times as high as in June 1956.

From the data presented above we may conclude that the normal cyclomorphosis of *Keratella tropica* in Fesafari starts with the appearance of the species as the floods subside in December. At this stage there is little or no left posterior spine. The left spine then increases in length and this is followed by a decrease, the detailed timing of which varies in different years. During the whole cycle the right posterior spine shows only small changes.

When correlations between the length of the lorica and the lengths of the spines in each sample are calculated some remarkable features are found (Table 5). The length of the right posterior spine is always positively correlated with the length of the lorica, but the left spine often shows no correlation with the length of the lorica, and in one sample a negative correlation was found. In yet other samples significant positive correlations were found.

The explanation of this bewildering array of correlation coefficients lies in the nature of the samples and the age composition of the population at the

TABLE 5

Seasonal variation in dimensions of *Keratella tropica*.

Date	Mean l. of lorica	Mean l. of left post. spine	Mean l. of right post. spine	Correlation (r) between lorica and left spine	Correlation (r) between lorica and right spine
	μ	μ	μ		
24 Feb 1954	94·74	1·18	60·74	0·06*	0·45
2 Mar 1954	95·88	3·12	65·30	0·31	0·68
9 Mar 1954	98·24	13·6	66·86	0·13*	0·66
16 Mar 1954	96·44	20·3	65·06	0·10*	0·65
23 Mar 1954	97·06	25·8	62·08	0·46	0·74
30 Mar 1954	97·20	25·5	62·78	0·26*	0·66
6 Apr 1954	99·02	30·5	64·48	0·12*	0·83
6 Jan 1955	95·58	0·0	54·46	0·0	0·28
23 Mar 1956	100·64	47·1	69·86	0·89	0·50
18 Apr 1956	99·34	26·46	65·08	0·36	0·61
7 May 1956	100·50	20·36	65·80	0·77	0·63
8 Dec 1956	100·90	1·73	61·17	—0·23*	0·33
8 Jan 1957	97·98	10·98	64·44	—0·30	0·51
3 Feb 1957	95·18	15·24	58·02	0·55	0·47
7 Mar 1957	94·44	6·02	58·18	0·11*	0·67
5 Apr 1957	93·60	0·28	54·88	0·15*	0·69

* Values not significantly different from 0 (P = 0·05).

time of sampling. Once a rotifer has become fully grown it cannot, save by accident and mutilation, alter the length of its spines, so that the important period during which spine length is determined lies early in the animal's life, perhaps even as far back as the period of maturation of the oocyte in the maternal ovary. At any one time the population will contain old individuals which have been mature for a week or two and whose spines were determined under different conditions from those of younger individuals in the same sample. When the population as a whole is showing rapid changes in the length of the left spine then any correlation between the length of the left spine and the length of the lorica can be expected to be small or non-existent. When the population is not showing rapid changes in the length of the left spine there is a chance for the population to become more homogeneous, and a positive correlation can develop. This is of course based on the assumption that in constant conditions the left spine would be positively correlated with the length of the lorica.

An examination of Table 5 confirms that breakdown of correlation between the length of the left spine and the length of the lorica is associated with periods of rapid change in the length of the left spine.

The lack of correlation on 24th February, 1954, was caused by most of the specimens lacking a left spine. As small left spines appeared a low positive correlation developed (2nd March, 1954), but this broke down when the left spine increased in length more rapidly (9th March, 1954). A positive correlation reappeared when the rate of change of the left spine began to slow down (23rd March, 1954). The breakdown of correlation on 30th March, 1954, preceded a further increase in the length of the left spine (6th April, 1954).

The data for 1956 and 1957 are at monthly intervals, but the same process of interpretation seems to be applicable. In March 1956 the population was probably at its peak length of left spine ; the length fell in the next sample, so that the spine had probably finshed increasing in length and a high positive correlation might be expected. The drop in correlation in the next sample (18th April, 1956) was clearly due to the change in length of the left spine, and the increase in correlation in the May sample can be explained by the much smaller decrease in length of this spine.

The negative correlation in January 1957 is just significant at the level $P = 0{\cdot}05$. It is difficult to explain, but it may be due to chance (1 in 20 of such samples could give negative correlations of this value in the absence of true correlation in the population) or it may be due to a rapid increase in length of the left spine so that smaller, younger animals would have relatively longer spines than older, larger animals which matured when conditions stimulating growth of the left spine were not so favourable. The next appearance of a positive correlation coincides with the peak of left spine length for the year (3rd February, 1957), and is followed by a breakdown of correlation as the left spine decreases.

It is clear from the data analysed above that we cannot hope to glean much about the relative growth of the left spine from the analysis of individual samples. The right posterior spine presents better opportunities for analysis. Fig. 18 shows the relationship between right spine length and lorica length in

the samples in which the right spine was at its longest (23rd March, 1956) and shortest (5th April, 1957)—actually the shortest mean right spine length was recorded on 1st January, 1955, but in this sample the correlation with lorica

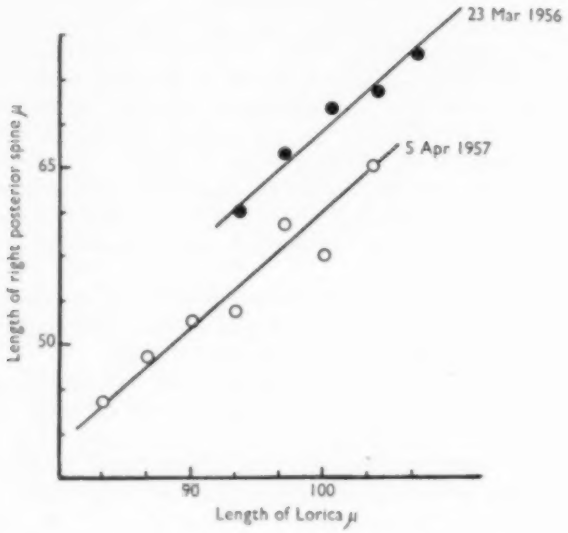

Fig. 18.—*Keratella tropica* : relation between length of lorica and length of right posterior spine. The points plotted are means of a varying number of animals (see frequency diagrams, Fig. 17).

length was unaccountably low so that the sample was not so favourable for analysis. The sample used for analysis does not differ significantly in its mean length of right spine from the lowest value, and if the data for 1st January, 1955, were plotted on Fig. 18 the points would lie around the lower line, but would be more scattered than those actually plotted. An interesting feature of this figure is that the two lines do not differ in slope, a fact which has been confirmed a comparison of the regression coefficients. The two lines do differ significantly ($P < 0{\cdot}0001$) in their heights and points of intercept of the axis. All the other samples have regression lines which lie between the two shown in Fig. 18.

Brachionus caudatus

The variation in form of this species was studied by measuring 100 specimens from each sample in which sufficient individuals were present ; only 30 were measured from the December 1956 sample. Only one of the posterior spines of each individual was measured because in most the spines were of equal length. If one spine was noticeably shorter than the other then the longer spine was measured.

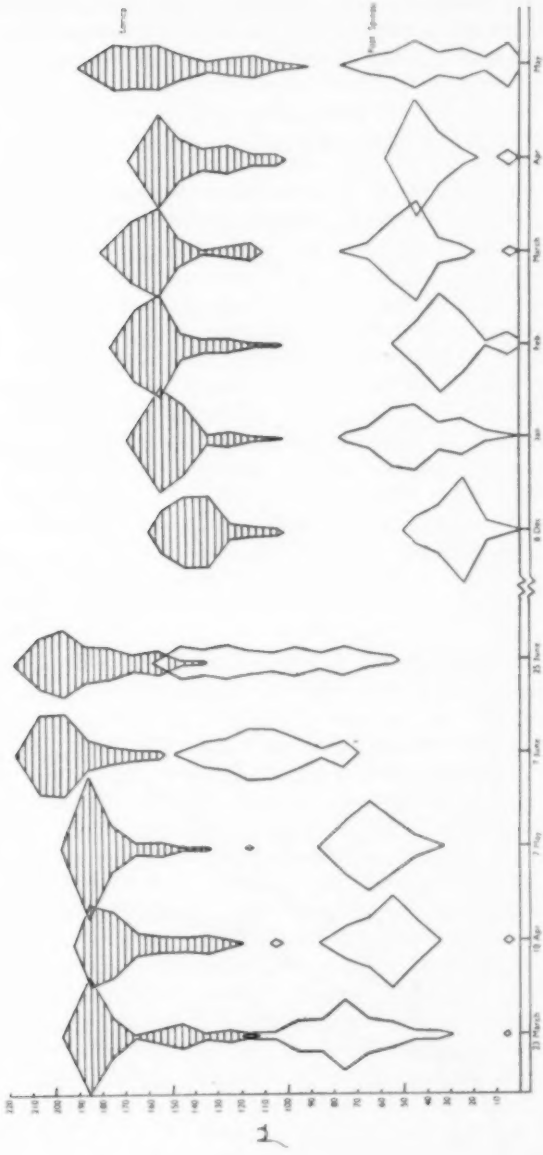

Fig. 19.—*Brachionus caudatus* : frequency distribution showing variation in dimensions during 1956 and 1957.

Fig. 19 shows that the length of the spines can vary enormously, but one never finds the majority of the population without spines ; individuals with very short or no spines are always in a distinct minority. Seasonal variation in spine length does not show as clear a cycle as that found with the left

posterior spine of *Keratella tropica*. There is a clear correlation between the length of the lorica and the length of the spines. The seasonal data show this fairly clearly, the only obvious exception being the February 1957 sample

TABLE 6

Seasonal variation in dimensions of *Brachionus caudatus*.

Date	Mean length of lorica μ	Mean length of posterior spines μ	Correlation (r) between lorica and posterior spines
23 Mar 1956	171·9	72·5	0·89
18 Apr 1956	167·5	56·7	0·70
7 May 1956	179·3	63·2	0·55
7 June 1956	194·1	109·0	0·69
25 June 1956	185·9	109·1	0·86
8 Dec 1956	140·0	28·3	0·48
8 Jan 1957	149·3	44·2	0·63
3 Feb 1957	154·2	31·8	0·47
7 Mar 1957	154·1	45·6	0·69
5 Apr 1957	144·1	39·8	0·65
17 May 1957	153·5	38·7	0·56

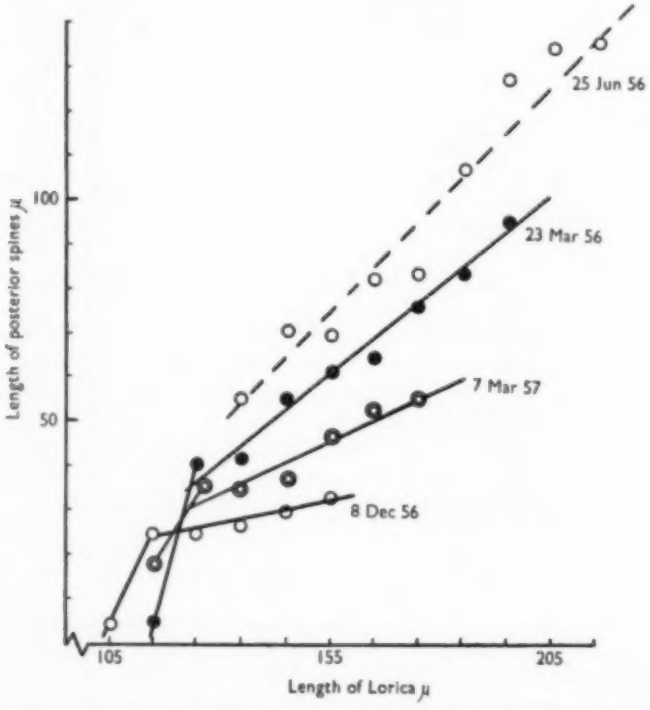

Fig. 20.—*Brachionus caudatus* : relation between length of lorica and lengths of posterior spines (see p. 519 for explanation).

when the mean lorica length increased slightly while the mean spine length decreased. Within each sample of 100 specimens the correlation between spine length and lorica length is generally strong as shown in Table 6.

When the relationship between spine length and lorica length is analysed it is found that the relationship varies with the mean length of the lorica. When the mean lorica length of a sample is high the spines are longer than when the mean lorica length is low ; the slope of the relationship is altered (Fig. 20) so that the smaller animals from a sample with a high mean lorica length have longer spines than animals of the same lorica length from samples with a low mean lorica length. At high lorical lengths the relationship is approximately linear, with the lines of all the samples converging back towards a point at which the lorica length would be about 105 μ and the spine length about 20 μ. This does not, however, happen. The lowermost points of three of the lines in Fig. 20 are much lower than one would expect from the trends of the other points. This may indicate that a critical size must be reached before the spines begin to grow rapidly ; all the individuals with no posterior spines had loricas less than 115 μ long. Once the critical size has been passed the length of the posterior spines varies with the mean size of the animals in the sample.

In Fig. 20 the lines have been fitted to the data by eye, but regression coefficients (b yx) have been calculated and compared ; these indicate that the slopes of the lines differ significantly at a level $P < 0{\cdot}001$.

DISCUSSION

The cyclomorphosis of *Keratella tropica* shows a distinct addition to the length of the left posterior spine in the early part of the season and a decrease in the length of this spine at the end of the season. This is similar to the cyclomorphosis of the European species *Keratella valga* as described by Hartmann (1918), whose results have been questioned by Ahlstrom (1943). In view of the results presented here concerning *K. tropica* there seems no valid reason for questioning the accuracy of Hartmann's observations.

When *Keratella tropica* and *Brachionus caudatus* are compared both similarities and differences are found. The two species are similar in that both had much longer spines in 1956 than in 1957. Clearly the environment can influence the growth of spines in both species in a similar manner. But the differences are great, particularly in relation to the changes in length of the left posterior spine of *K. tropica*. It may be that the right spine of this species is peculiar in that it is fairly constant in length and does not show the large variations in length which are found in the left spine and in both the posterior spines of *B. caudatus*. The two species also differ in their relationship between spine length and seasonal occurrence. Although both had longer spines in 1956, *K. tropica* decreased the length of its left posterior spine and disappeared from the plankton by the end of June, while *B. caudatus* persisted throughout June and increased the lengths of its posterior spines.

The problems of spine length in *Keratella tropica* are more complex than in *Brachionus caudatus*. The large variation in the left spine of *K. tropica* while the right spine remains fairly constant in length can only mean that

there must be some advantage in retaining the right spine. It also poses a problem in relation to the causal mechanism of cyclomorphosis. The environment probably controls the variations of the left spine, but internal factors must surely be responsible for the retention of the right spine. Fig. 18 shows that the length of the right spine varies with the length of the lorica ; this can be interpreted as showing that a larger body produces more of the internal factor influencing spine growth. The difference between the right and the left spine implies unequal distribution of this factor. The data concerning *B. caudatus* may also be related to an internal factor influencing spine growth. Here too the spines vary with the length of the lorica and seem to be influenced by the growth rate of the rotifer. The greater spine lengths achieved by animals which are growing more rapidly may be attributed to a more rapid production of the internal factor controlling spine growth.

It seems reasonable to assume that a high rate of growth will occur when the rotifer is well fed. If this is so then it is difficult to reconcile the relation between spine length and lorica length with the results of Büchner, Mulzer & Rauh (1957) who maintain that poor feeding enhances spine growth in *Keratella cochlearis* and *Brachionus calyciflorus* (= *pala*). They did not, however, actually measure the spines of the animals they studied, and it is uncertain whether their control of feeding was adequate to eliminate chance results due to bacteria, which might form suitable food for rotifers.

Among the possible factors which may control the growth of rotifers both the amount and the nature of the food available should be considered. It is known for instance that some species of algae are better than others of the same genus as rotifer food (Pourriot, 1957). Oxygen, pH and temperature may also be involved. Dissolved oxygen is known to be a factor in the complex controlling the growth of other planktonic animals such as *Daphnia* (Green, 1956). Hydrogen ion concentration is well known to be of importance in governing the distribution of rotifer species ; it seems likely that there is an optimum pH for the growth of particular species. An increase in temperature would accelerate the rate of growth, but it may also accelerate the onset of maturity so that the rotifer may become mature at a smaller body size than if it grew more slowly at a lower temperature. It would be possible for the effect of an increase in temperature on spine growth to vary according to whether it accelerated maturation more or less in relation to growth.

It is worth noting that the decrease in length of the left spine of *K. tropica*, from March to May 1956, was undergone while the temperature remained consistently between 26 and 29°C. The complete cycle of increase and decrease, from December 1956 to April 1957, happened when the temperature first of all fell from 21°C. in December to 16°C. in January and then rose steadily to 27°C. at the beginning of April. There is no obvious correlation between the cycle of *K. tropica* and the temperature of its environment.

It is clear from the data presented above that the factors controlling the variation in spine length in rotifers are likely to be complex, and that simple theories, such as those of Wesenberg-Lund (1900, 1908) and Ostwald (1902) cannot be applied. There is no simple relation between spine length and temperature such as would be demanded by these theories. Investigations

in Europe have shown that the posterior spines of *Keratella quadrata* decrease in length during the warmer months (*cf.* Carlin, 1943), so that in this species at least there is no question of increased spine length compensating for a decrease in the viscosity of water as temperature rises.

Gallagher (1957) claims to have established a positive correlation between temperature and posterior spine length in a North American population of *Keratella cochlearis*. This claim deserves scrutiny because it is in direct opposition to the classical work of Lauterborn (1903), who found a decrease in the length of the posterior spine of this species during the summer months in Germany. Gallagher's correlation was calculated between mean air temperature of the twenty-four hours in which his collections were made and the mean spine length of a varying number of animals. The use of mean spine length in this way is not a valid statistical procedure, since it automatically removes much of the variance which a correlation coefficient is intended to estimate. Even if the use of mean spine length was acceptable the significance of some of the means given by Gallagher is open to question. The range of mean spine length which he gives is small (22–36 μ), and the lowest of these is based on but four individuals. The standard error of this mean is given as 8·51, which, unless it is a typographical error, is so great as to exclude this particular mean from having any significance in relation to the rest of his data. There are significant differences between some of his mean values, perhaps the most striking of these is the mean spine length of 32 μ when the mean air temperature was 7·2°C. which is significantly higher than the mean spine length of 23 μ which was recorded when the mean air temperature was 9·4°C. Discrepancies such as these are sufficient to invalidate Gallagher's conclusion that there is a positive correlation between air temperature and spine length.

As rotifers live in water, and water temperatures are generally less variable than air temperatures, one might more justifiably seek a correlation between water temperature and spine length, but Gallagher admits that if the correlation is calculated between water temperature and spine length then there is no significant correlation at a level of $P = 0{\cdot}05$.

It would also seem to be desirable to consider spine length in relation to the size of the animal bearing the spine ; Gallagher provides no data of this type.

The most detailed and thorough work on the cyclomorphosis of rotifers is that of Carlin (1943) who showed that *Kellicottia longispina*, *Keratella quadrata* and *Keratella stipitata* (= *cochlearis*) decrease the length of their spines when the water temperature is at its highest. Carlin reconciles these findings with ideas of flotation by considering the turbulence of the water. In the warmer weather the viscosity of the water will be lowered so that turbulence might be expected to be greater for a given amount of energy expended in producing a current (for instance by wind or inflow into a pond). An increase in turbulence would tend to keep the rotifers afloat, so that their need for long processes would be reduced. In winter the viscosity of the water will be higher and turbulence will be weaker, lending less support to the rotifers so that their spines need to be longer. This idea may be capable of wider application, but

it is a teleological explanation offering only a partial explanation of cyclomorphosis.

Any future approach to the problem of cyclomorphosis in rotifers must consider the length of the spines in relation to the body size of the rotifer. Margalef (1947) took a step in this direction when he used logarithmic scales to plot the spine lengths and lorica lengths of *Keratella quadrata*, as measured by various other authors, and found that the relationship could be expressed as a straight line. This indicates that the longer spines are a result of allometric growth. It would be of interest to plot similar data for *K. quadrata* on a seasonal basis to see if there is any parallel to the relationships described on p. 519 for *Brachionus caudatus*.

It may be unwise to seek a unifying explanation of variation in all the various protuberances in diverse families and species of rotifers. The specific line of approach seems to be the most profitable at present. Only when there is sufficient information available concerning the relationship between environmental factors and seasonal forms of a considerable range of species will it be worthwhile examining the possibility of a general explanation.

The two species described in this paper illustrate the difficulties that any general explanation will encounter. It will have to explain why two species in the same habitat, both having two posterior spines, differ in that one varies both its spines in a similar manner, while the other varies the left spine without much variation in the right spine. Two lines for future study may be suggested. First a study of the relationship between growth and the development of spines to determine the environmental complex of factors controlling the relationship. The second line of approach might deal with the physical effects of variation in length of spines on the locomotion of rotifers, particularly in relation to the turbulence of water. This might throw some light on the significance of cyclomorphosis as an ecological and evolutionary phenomenon

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NEW GREGARINES PARASITIC IN LEPISMATIDS FROM CEYLON

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(With 23 figures in the text)

Three new species of cephaline gregarine from lepismatid insects of Ceylon are described in this paper. The relationship of these new species to other species belonging to the same genera is discussed. A list is given of the gregarine species so far recorded from Apterygota throughout the world.

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INTRODUCTION

Some preliminary facts concerning the eugregarines of Thysanura from Ceylon and England were reported earlier (Crusz, 1957). Two of the three new species of cephaline gregarine from Ceylonese lepismatids were found by me to co-exist with *Garnhamia aciculata* (Bhatia, 1938) Crusz, 1957, in *Peliolepisma calvum*, and one is named in honour of Mr D. R. R. Burt, my former teacher and the first professor of Zoology in the University of Ceylon. Two were found co-existing in *Ctenolepisma nigrum* and one is named in honour of Professor J. J. C. Buckley, my teacher at the London School of Hygiene and Tropical Medicine. One new species was found in the midgut of both *Peliolepisma calvum* and *Ctenolepisma nigrum*.

MATERIAL AND METHODS

Specimens of *Peliolepisma calvum* and *Ctenolepisma nigrum* were collected from various localities in Ceylon and reared in covered glass troughs under optimum conditions of temperature and humidity on the lines recommended by Spencer (1937) and Adams (1937). They were fed on finely ground, commercial rolled oats (Quaker Oats). Room temperatures in Colombo throughout the year were ideally suited to these insects. Even species like *Lepisma saccharinum* from England and *Ctenolepisma longicaudatum* from Melbourne, Australia, which are being bred for experimental and comparative studies, have been thriving well under laboratory conditions in Colombo.

Specimens belonging to the same species and collected from the same locality were reared as a separate culture. The value of this procedure became apparent when it was discovered that *Ctenolepisma nigrum* from Hingurakgoda, at first thought to be *Peliolepisma calvum* owing to close superficial resemblance, harboured a species of *Colepismatophila* which produced spores distinctly larger than those of the species from *P. calvum* in Colombo and other west-coast towns.

Clean, gregarine-free cultures of silverfish were obtained by careful segregation of eggs. In this way it was possible to follow the life-history of the gregarine species by experimental infection and also perform cross-infection experiments between different species of silverfish. The results of these latter experiments were all negative and inconclusive. It is hoped to give a report of them as more evidence is accumulated.

The gregarines were studied from freshly caught silverfish and from those reared in the laboratory. The midguts containing them were slit open and the contents teased out in 0·75 per cent salt solution. Bits of broken cover-glass were inserted between slide and cover-glass to prevent distortion and crushing of the gregarines. The parasites were then quickly drawn under the camera lucida. Midguts were also fixed in Bouin's or Carnoy's fluid, embedded in Celloidin-Paraffin (Peterfi's method), serially sectioned 6–8 microns thick, stained in Heidenhain's or Ehrlich's haematoxylin and counterstained in eosin. Cysts (gametocysts) and spores (oocysts) were freed from faeces in water, under the microscope, and their structure and dehiscence were noted. Camera lucida drawings were made of all these stages for purposes of measurement and permanent record.

The identification of the silverfish was done by Dr P. Wygodzinsky of Tucuman, Argentina, the well-known authority on this group of insects. *Peliolepisma calvum* is a common domestic silverfish in Ceylon, but not as common as *Acrotelsa collaris*. *Ctenolepisma nigrum* from Hingurakgoda seems to be closely related to *P. calvum*.

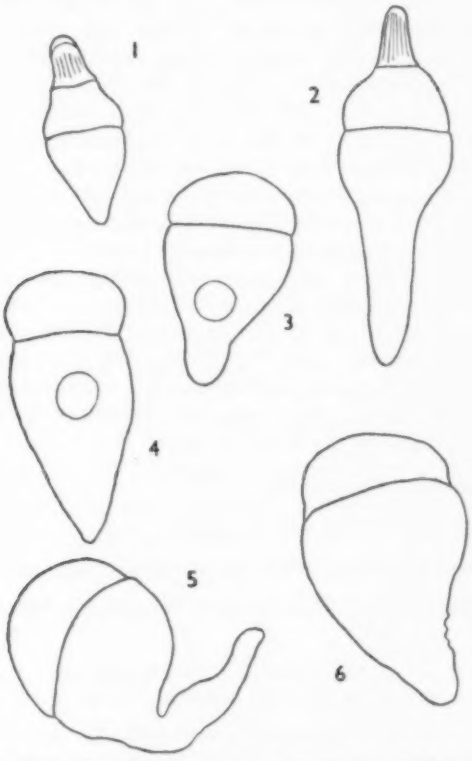
COLEPISMATOPHILA BURTI sp. n.

(Figs. 1–6 and 15)

Cephalont : The earliest stages of the life-cycle are passed within the epithelial cells of the midgut. With the formation of an epimerite the cephalont becomes extracellular. A septum between protomerite and deutomerite develops later, the nucleus being confined to the deutomerite. The fully-formed cephalont assumes the typical structure of a cephaline gregarine (Figs. 1 and 2). The epimerite is elongate and thimble-shaped, measuring 26·5–36·9 by 16·2–19·5*. The protomerite is sub-hemispherical and present throughout the cephalont and sporont stages. The deutomerite is conoid and broad-based, narrowing posteriorly more abruptly than in *Lepismatophila orientalis* sp. n. The cytoplasm of the three regions is more translucent in the younger stages, but becomes densely and darkly granular later on, especially in the deutomerite in the region surrounding the nucleus. The protomerite has less dense cytoplasm than the deutomerite, but in fixed

* All measurements, unless otherwise stated, are in microns.

and stained preparations it shows a coarse structure and stains more deeply than the deutomerite. The epimerite has a densely granular cytoplasm, showing a fine structure when fixed and stained. The whole body is invested by a pellicle, thin in the epimerite and protomerite, thick and refractive in the deutomerite. The nucleus is 18·1–24·4 in diameter and situated in the wide part of the deutomerite, a short distance from the septum. The karyosome can be clearly seen only in stained preparations. It varies in shape from spheroid to ovoid or ellipsoid, and sometimes even appears broken up into a number of smaller bodies.



Figs. 1–6.—*Colepismatophila burti* sp. n. 1 & 2. Free cephalonts. 3–6. Sporonts.

Sporont : The cephalonts free themselves from the intestinal wall with their epimerites still attached and become sporonts. The epimerites gradually lose their granular appearance and disappear. The sporonts (Figs. 3–6), which are solitary and darkly opaque, then pass down the midgut between intestinal wall and peritrophic membrane. As Cornwall (1915) observed for *Lepismatophila cornwalli* (Bhatia, 1938) and contrary to Lindsay's statement (1939) concerning *L. ctenolepismae*, I have on occasion seen unassociated sporonts in the hindgut and even in the faeces where they were still very much

alive. This has been noted by me even for the other gregarine species of *Peliolepisma calvum*. The sporonts measure, Length of Protomerite (LP) 12·9–35·6, Length of Deutomerite (LD) 37·1–168·7, Width of Protomerite (WP) 29·7–94·4, Width of Deutomerite (WD) 37·1–97·5. Association between sporonts, protomerite to protomerite, takes place nearer the posterior end of the midgut. A cyst wall is secreted and the rounded cyst passes into the hindgut.

Cysts and spores : The cysts appear pearly white in colour under a hand lens and are passed to the outside in the faeces, to which they are attached, usually one to each faecal pellet. They are thin-walled, spheroid to ovoid or ellipsoid, and measure 138·7 by 126·9. A fresh cyst, when freed from faecal matter and examined in water or saline under the microscope, is seen to be colourless like the spores within it. But as the cysts and spores ripen they become dark brown in colour, probably due to a phenolic tanning process (Ratnayake, 1960). The wall of the cyst is characteristically pitted and grooved. The spores formed within it are concentrated on one side of the cyst, while the other side is occupied by residual cytoplasm and globules.

Each spore (Fig. 15) is a sub-hemispherical body carrying, at opposite ends, two curving filamentous processes extending in opposite directions and connecting temporarily with similar processes of adjoining spores. Thus a coiled chain of spores is formed within the cyst. Each spore-process of this species is typically about the length of, or a little shorter than, the main body of the spore. The spores measure 12·4–15·6 by 6·7–8·6, and each spore-process 8·0–15·3 by 0·9–1·3. The spores are released by rupture and recurling of the cyst wall, the rupture taking place along the grooves of the cyst wall. This species is named in honour of Mr D. R. R. Burt.

Host : ***Peliolepisma calvum*** Ritter, 1911.

Habitat : Midgut, including sacculi (caeca).

Locality : Houses in Colombo, Puttalam, Hikkaduwa and Galle (Ceylon).

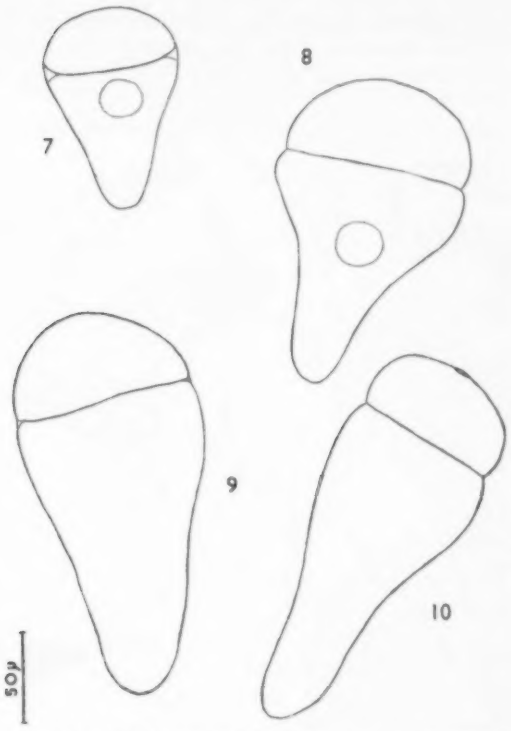
Types: Prepared slides in collection of Department of Zoology, University of Ceylon.

COLEPISMATOPHILA BUCKLEYI sp. n.

(Figs. 7–13 and 16)

The silverfish *Ctenolepisma nigrum* from Hingurakgoda, in the North Central Province dry zone of Ceylon, was found to harbour a gregarine whose stages follow closely those of *Colepismatophila burti* sp. n., but there are marked differences in regard to dimensions, particularly of the spores (Fig. 16). This gregarine is therefore considered as belonging to a new species, *Colepismatophila buckleyi*, whose dimensions are as follows : LP 31·9–51·9, LD 75·6–179·4, WP 72·5–106·2, WD 73·1–110·6. Epimerite 27·6–31·2 by 8·6–20·0. Nucleus 23·1–25·0 in diameter. Cysts 196·9–327·0 by 143·7–290·7. Spores 15·0–20·5 by 7·7–9·8. Spore-processes 10·1–16·2 by 1·2.

This species is named in honour of Professor J. J. C. Buckley.



Figs. 7–10.—*Colepismatophila buckleyi* sp. n. Sporonts.

Host : Ctenolepisma nigrum (Oudemans, 1890) Silvestri, 1913.

Habitat : Midgut, including sacculi.

Locality : Houses in Hingurakgoda, N.C.P. (Ceylon).

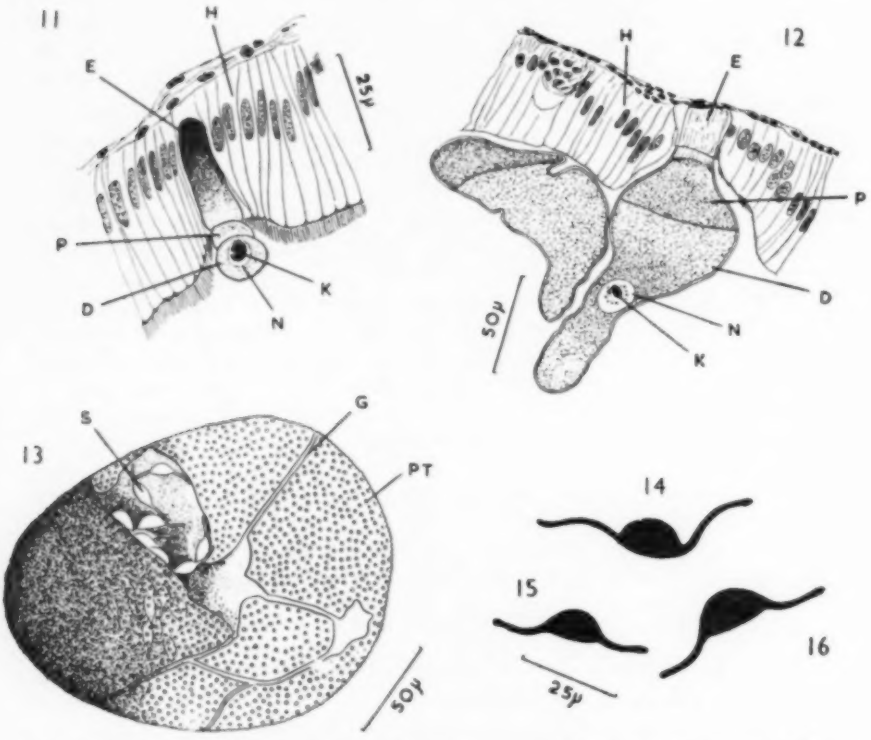
Types : Prepared slides in collection of Department of Zoology, University of Ceylon.

LEPISMATOPHILA ORIENTALIS sp. n.
(Figs. 17–21)

The stages in the life-cycle of *Lepismatophila orientalis* sp. n. are very similar to those of other species of *Lepismatophila* described by Adams & Travis (1935), Lindsay (1939) and Tuzet, Manier & Ormières (1952) ; nor do they differ in their essential features from those of the *Colepismatophila* spp. described above.

The fully formed cephalont (Figs. 17 and 20) of *Lepismatophila orientalis* has a smooth, globular and sessile epimerite, 8·7–11·2 in diameter. The epimerite often appears slightly flattened and sub-hemispherical, and then measures 8·6–9·9 long and 10·5–14·8 broad. The protomerite, like that of *L. cornwalli* (Bhatia, 1938), is elongate and taller than in other species, becoming sub-hemispherical only later on, in the mature sporont. The deutomerite

is narrow-based and tapering posteriorly. At the posterior end is sometimes seen a cluster of short processes (Figs. 17 and 20). The dimensions of free individuals are : LP 13·8–42·5, LD 42·2–246·2, WP 28·1–95·0 ,WD 27·7–95·0.



Figs. 11–13 & 16.—*Colepismatophila buckleyi* sp. n. 11. Very young cephalont attached to intestinal epithelium of *Ctenolepisma nigrum* (from serial section, 6 microns thick, stained in Heidenhain's haematoxylin and eosin). 12. Older cephalont still attached (from another series, cut and stained as above). 13. Pitted and grooved cyst with immature spores. 16. Mature spore.
H.—Host cell. E.—Epimerite. P.—Protomerite. D.—Deutomerite. N.—Nucleus. K.—Karyosome. S.—Spore. G.—Groove. PT.—Pit.

Fig. 14.—*Colepismatophila watsonae*. Mature spore from faeces of *Acrotelsa collaris*.

Fig. 15.—*Colepismatophila burti* sp. n. Mature spore.

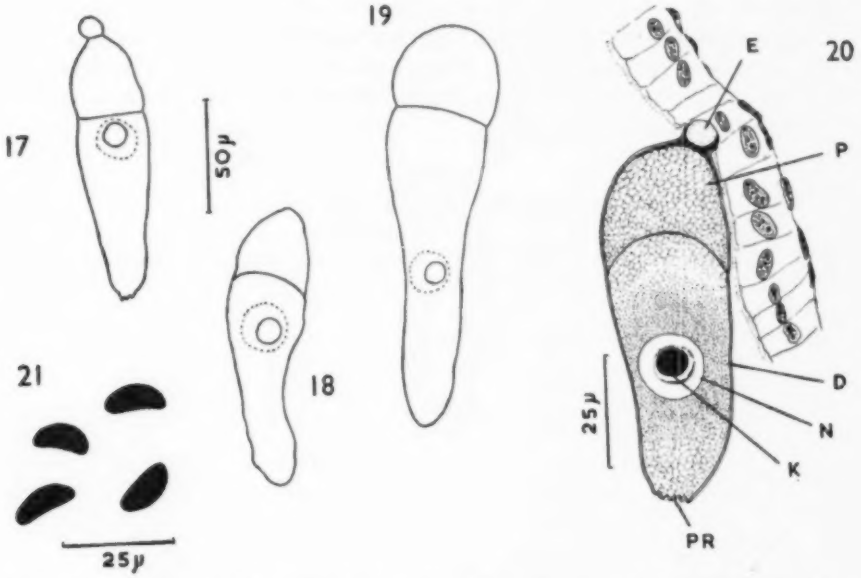
The nucleus measures 11·3–30·0 in diameter. There is a distinct, spherical karyosome, 6·0–12·5 in diameter. The cysts are thin-walled, pitted and grooved and vary in shape from spheroid (458 in diameter) to ovoid or ellipsoid (143·7 by 121·2). The spores (Fig. 21) are smooth-walled, one side being more convex than the other, and they lack the spore-processes characteristic of *Colepismatophila* spp. They measure 11·3–14·1 by 4·3–6·4 in the forms from *Peliolepisma calvum* and 11·6–14·7 by 4·3–5·8 in those from *Ctenolepisma nigrum*. Both cysts and spores are colourless when first formed, but darken with age.

Hosts : *Peliolepisma calvum* and *Ctenolepisma nigrum*.

Habitat : Midgut, including sacculi.

Localities : Houses in Colombo (*P. calvum*) and Hingurakgoda (*C. nigrum*).

Types : Prepared slides in collection of Department of Zoology, University of Ceylon.



Figs. 17–21.—*Lepismatophila orientalis* sp. n. 17. Free cephalont. 18 & 19. Sporonts. 20. Cephalont attached to intestinal epithelium of *Peliolepisma calvum*. (From serial section, 6 microns thick, stained in Ehrlich's haematoxylin and eosin). PR.—Processes. (Other lettering as before.) 21. Mature spores.

DISCUSSION

The two new species *Colepismatophila burti* and *C. buckleyi* are closely related to *Colepismatophila watsonae* Adams & Travis, 1935, as shown by the various stages in their life-cycles. But they are both markedly different from *C. watsonae* in the shape of their epimerites and in dimensions, especially those of the spores (Figs. 15 and 16) which have much shorter processes relative to spore body size. This indicates specific difference between the two new species and *C. watsonae* (Fig. 14).

It appears to be somewhat difficult at first to regard *C. buckleyi* as a species distinct from *C. burti*, since they both co-exist with *Lepismatophila orientalis* sp. n. and also in view of the tendency shown by a gregarine species to differ in size in different hosts (Théodoridès, 1955 a and b). This tendency for size difference is true of most of the stages of a gregarine's life-cycle. But Filipponi (1954) has shown by careful statistical analysis of dimensions of various stages

in the life-cycle of *Protomagalhaensia marottai*, in field and laboratory populations of larvae and adults of *Scaurus striatus*, that spore (oocyst) dimensions, particularly spore-length, are the most stable and most representative character of the species and varied negligibly in different hosts. On these grounds *Colepismatophila buckleyi* is considered to be a valid species because its spores differ significantly from those of *C. burti*. Table 1 and Fig. 22 show frequency distribution for lengths of 100 spores taken at random of each of these two species.

Lepismatophila orientalis sp. n. has the smallest spores yet recorded for any species of *Lepismatophila*. They resemble those of *L. ctenolepismae* Lindsay, 1939, and *L. campodeae* Tuzet, Manier & Ormières, 1952, in the

TABLE 1

Frequency distributions of length of spores.

SPORE LENGTH (MICRONS)	FREQUENCY			
	C. burti	*C. buckleyi*	*L. orientalis* (from *P. calvum*)	*L. orientalis* (from *C. nigrum*)
11·3	–	–	5	–
11·6	–	–	8	1
11·9	–	–	13	1
12·3	–	–	29	–
12·4	1	–	–	–
12·6	2	–	6	8
12·7	2	–	–	–
12·9	10	–	23	7
13·0	2	–	–	–
13·2	6	–	8	20
13·3	2	–	–	–
13·5	4	–	5	13
13·7	3	–	–	–
13·8	16	–	1	23
14·1	20	–	2	20
14·4	8	–	–	5
14·7	12	–	–	2
15·0	6	1	–	–
15·3	5	–	–	–
15·6	1	3	–	–
15·9	–	3	–	–
16·2	–	7	–	–
16·5	–	22	–	–
16·8	–	13	–	–
17·2	–	18	–	–
17·5	–	11	–	–
17·8	–	8	–	–
18·1	–	8	–	–
18·4	–	4	–	–
19·0	–	1	–	–
20·5	–	1	–	–
TOTAL	100	100	100	100

presence of a smooth wall and in one side being more convex than the other, but the spores of the latter two species are well over 14 microns in length.

The cephalont of *L. orientalis* resembles closely that of *L. cornwalli* (Bhatia, 1938) as figured by Cornwall (1915). But no measurements of any of the stages of the latter species are available for comparison. Furthermore, its spores are described as having thick and sculptured walls. *Lepismatophila orientalis*, therefore, represents a species quite distinct from other species of the genus. Table 1 and Fig. 23 show frequency distribution for lengths of 100 spores of *L. orientalis* taken from each of its two lepismatid hosts.

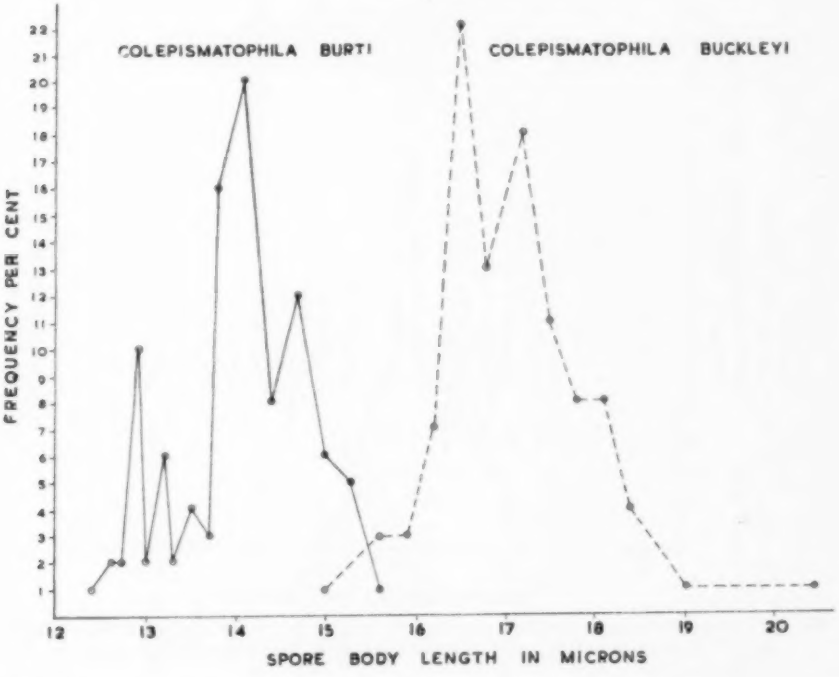


Fig. 22.—Diagram showing frequency distributions of spore body lengths of *Colepismatophila burti* and *C. buckleyi*. (100 spores of each species.)

ACKNOWLEDGMENTS

My thanks are due to Dr A. J. Marcus Fernando of Hingurakgoda, Mr Edward Jansz of Galle and Mr K. Piyadasa of Hikkaduwa for the kind facilities they gave me for collecting silverfish in their respective localities, and to Master Culani Fernando of Barnes Place, Colombo, for having collected a single female specimen of *Ctenolepisma longicaudatum* harbouring *Garnhamia aciculata*.

I am also grateful to the following who, with much trouble and cost to themselves, sent me living and fixed specimens of the species noted against

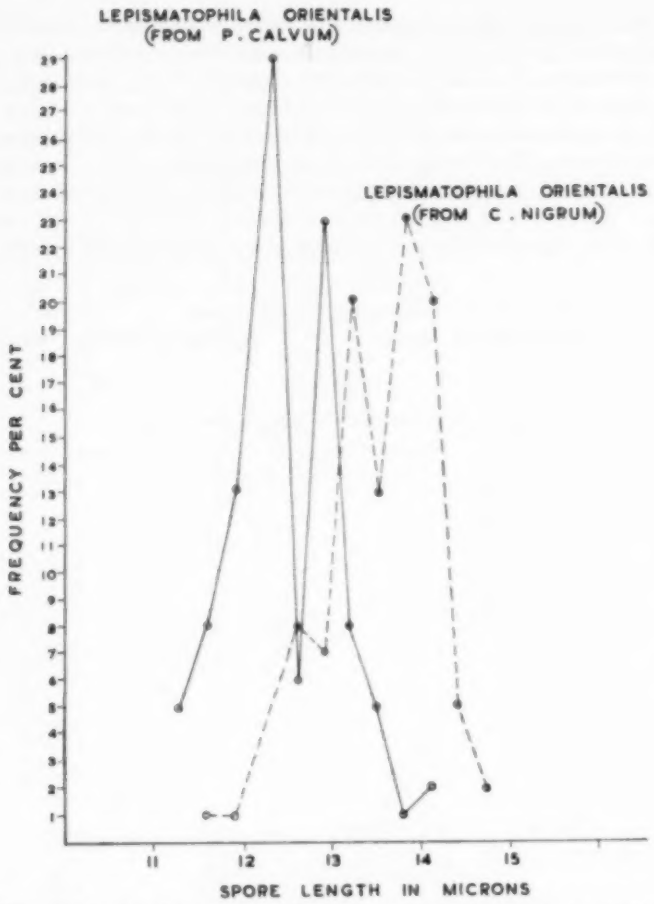


Fig. 23.—Diagram showing frequency distributions of spore lengths of *Lepismatophila orientalis* from *Peliolepisma calvum* and *Ctenolepisma nigrum*. (100 spores of the gregarine from each host.)

their names : Acting Professor F. H. Drummond of Melbourne University (*Ctenolepisma longicaudatum*), Dr P. Wygodzinsky of Argentina (*C. longicaudatum*), Professor Harvey Sweetman of Massachusetts University (faeces of *Lepismodes inquilinus* with gregarine spores) and Mr G. A. Brett and Mr A. G. Histed of the Infestation Control Division, Tolworth, England (*Lepisma saccharinum*).

Professor W. Fernando, Head of the Department of Zoology, and Sir Nicholas Attygalle, Vice-Chancellor, University of Ceylon, gave me all the facilities and encouragement for the pursuit of these studies, and Dr H. E. Fernando, Entomologist, Government Department of Agriculture, gave me the necessary permits for importing live specimens of *C. longicaudatum* and *L. saccharinum*. To all of them I am much indebted.

CEPHALINE GREGARINES OF APTERYGOTA

PARASITE	HOST	LOCALITY
	ORDER : COLLEMBOLA	
1. *Gigaductus podurae* (Léger, 1892) Grassé, 1953	*Orchesella villosa* (= *Podura villosa*)	France
2. *Gregarina wellmeri* Zwetkow, 1929	*Allacma fusca* (= *Sminthurus fuscus*)	Germany (E. Prussia & Silesia), Russia (Peterhof).
	Tetrodontophora bielanensis	Germany (Silesia).
	ORDER : DIPLURA	
3. *Lepismatophila campodeae* Tuzet, Manier & Ormières, 1952	*Campodea monspessulana* Condé, 1953	France
4. Unidentified gregarine, Marten, 1939	*Campodea taunica*	Germany
	ORDER : THYSANURA	
5. *Hyalospora affinis* Schneider, 1882	*Machilis cylindrica*	France
6. *Hyalospora roscoviana* Schneider, 1875	*Halomachilis maritimus* (= *Petrobius maritimus*)	France
	Machilis tenuis	France
7. *Hyalospora volsella* Tuzet & Ormières, 1956	*Atelura pseudolepisma*	France
8. *Dinematospora grassei* Tuzet & Ormières, 1954	*Machilis tenuis*	France
9. *Gregarina lagenoides* (Léger, 1892) Labbé, 1899	*Lepisma saccharinum*	France, Germany (E. Prussia), *England**
10. *Garnhamia aciculata* (Bhatia, 1938) Crusz, 1957	*Ctenolepisma* or *Acrotelsa* sp. ?	India
	Ctenolepisma longicaudatum	Australia, Tasmania, *Ceylon*, *Argentina*
	Peliolepisma calvum	*Ceylon*
	Acrotelsa collaris	*Ceylon*
11. *Lepismatophila thermobiae* Adams & Travis, 1935	*Lepismodes inquilinus* (= *Thermobia domestica*)	U.S.A., *England*
	Lepisma saccharinum	*England*
	Acrotelsa collaris	*Ceylon*
12. *Lepismatophila cornwalli* (Bhatia, 1938)	*Ctenolepisma* or *Acrotelsa* sp. ?	India
13. *Lepismatophila orientalis* sp. n.	*Peliolepisma calvum*	*Ceylon*
	Ctenolepisma nigrum	*Ceylon*
14. *Lepismatophila ctenolepismae* Lindsay, 1939	*Ctenolepisma longicaudatum*	Australia, Tasmania, *Argentina*
	Ctenolepisma lineatum var. *piliferum*.	Australia
	Lepismodes aegyptiacus	Australia
15. *Lepismatophila parva* Tuzet, Manier & Ormières, 1952	*Ctenolepisma lineatum*	France
16. *Colepismatophila watsonae* Adams & Travis, 1935	*Lepismodes inquilinus*	U.S.A.
	Acrotelsa collaris	*Ceylon*
17. *Colepismatophila burti* sp. n.	*Peliolepisma calvum*	*Ceylon*
18. *Colepismatophila buckleyi* sp. n.	*Ctenolepisma nigrum*	*Ceylon*
19. Unidentified gregarine, Lindsay, 1939	*Lepisma saccharinum*	Australia

* Localities in italics are those recorded by me for the corresponding gregarine species.

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OBSERVATIONS ON THE TECTIBRANCH *RINGICULA BUCCINEA* (BROCCHI)

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[Accepted 8th March, 1960]

(With 5 figures in the text)

Ringicula buccinea is an opisthobranch mollusc with a comparatively large external shell which burrows in muddy sand using its foot and cephalic disc. The latter helps to exclude sand from the mantle cavity, is produced into an inhalant siphon dorsally and is fused with the foot laterally. The gill is reduced and the main pallial water current is an exhalant one. There is no exogyrous caecum.

Glands open just within the lips and the buccal cavity contains paired jaws and a reduced buccal mass and radula. Into it open the small salivary glands. The oesophagus has neither glands nor crushing plates. The stomach is large with the oesophagus, intestine and liver ducts opening close together to a thin-walled anterior chamber, whereas a larger posterior chamber has thick, muscular walls and a cuticularized epithelium. Interstitial copepods and Foraminifera are collected for food and crushed in the triturating region.

The rectum and pallial genital oviduct lie in the floor of the mantle cavity. A single duct carries both sperm and ova to the mouth of the cavity ; a bursa copulatrix and receptaculum are associated with it. The penis is retracted into a sheath which opens on the head and is associated with a prostate gland.

Discussion of these aspects of the animal's structure confirms its position as a primitive tectibranch which is specialized for burrowing and also shows affinities with the basommatophoran pulmonates.

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INTRODUCTION

Specimens of *Ringicula buccinea* (Brocchi) were dredged at St. Jean-de-Luz, B.P., France, from muddy sand. I am indebted to B. S. Kisch, Esq., C.I.E., for the opportunity of obtaining and studying the animals alive and for identifying the species.

Ringicula, which is one of the most primitive opisthobranchs, is represented by a number of species in the warmer seas, but little is known about them. They are classified in the Ringiculidae, the second family of Thiele's stirps Cephalaspidea (Thiele, 1931). The external features of *R. caeca* were described by Annandale & Prashad (1919) and the anatomy of *R. conformis* by Pelseneer (1925). These descriptions, however, are too brief to show the

relationships with related gastropods, and Pelseneer's account suggests that there are important differences between *R. conformis* and *R. buccinea*.

EXTERNAL FEATURES

The genus *Ringicula* is closely related to *Acteon*, though it has fewer prosobranch affinities. Both have a large shell into which the snail can withdraw completely ; only in *Acteon* is there an operculum to seal the opening. The body whorl is deep and the aperture elongated along the right side to a length more than half the height of the shell. In *Ringicula* the columella is stout and in *R. buccinea* it has three longitudinal folds which project as teeth at the columellar lip. The shell is white and glossy measuring in this species about 4 mm. high, and the exposed tissues of the body are devoid of pigmentation.

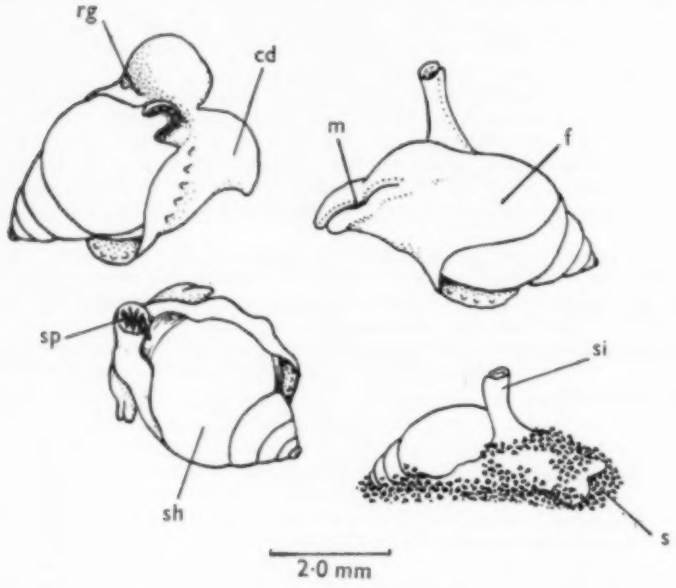

Fig. 1.—*Ringicula buccinea* : external features.
cd, cephalic disc ; f, foot ; m, position of mouth ; rg, repugnatorial gland ; s, sand particles ; sh, shell ; si, siphon of cephalic disc ; sp, sensory papillae at entrance to siphon.

Even the eye pigment is not visible for the eyes are sunken from the surface. The snail burrows through the muddy sand in search of food, but unlike *Acteon* it explores only the upper layer, and a short siphon (si, Fig. 1), leading to the siphonal canal of the shell, is then extended to the surface to maintain a flow of water through the mantle cavity. The siphon is a median extension of the cephalic disc (cd). The disc is formed by the expanded tentacles and fused laterally with the foot so that together they comprise an extensible sleeve which is reflected over the body whorl of the shell, closing off the opening to the mantle cavity. The siphon is an incomplete tube and when the animal is

inactive it is opened out and contracted to a negligible length. When it is extended a ring of six papillae can be seen just within the opening (sp). The cephalic disc has large repugnatorial glands (rg) arranged in a row parallel to its border, and if the animal is irritated the ducts of the glands project as nipples from the surface, and then a sudden ejection of secretion is effected by the contraction of muscles which surround each gland. The fluid is toxic to small animals. The detailed structure of the glands is similar to those figured for *Siphonaria* sp. (Fretter & Graham, 1954) except that the muscular coat is thicker.

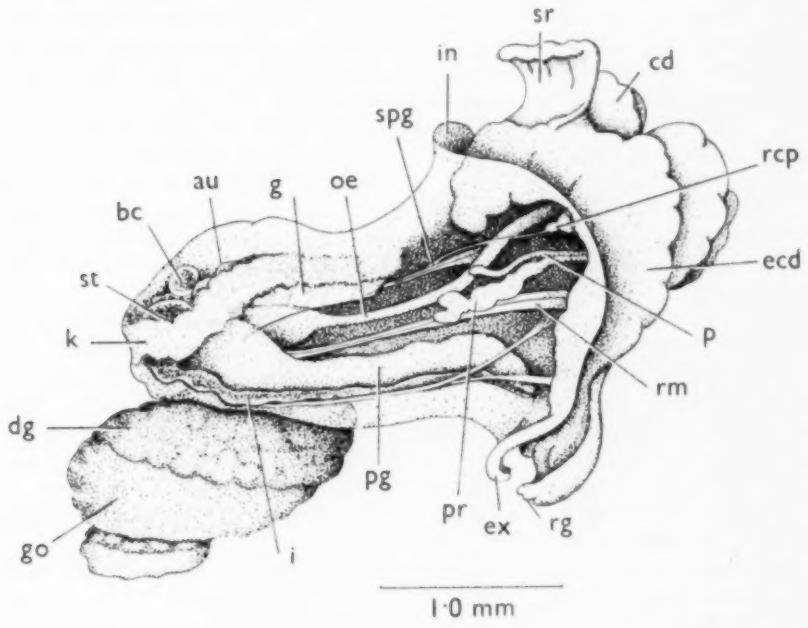

Fig. 2.—*Ringicula buccinea* : whole animal, shell removed, seen from the right. Fixed in Bouin, cleared in cedarwood oil.

au, auricle ; bc, bursa copulatrix ; cd, cephalic disc ; dg, digestive gland ; ecd, edge of cephalic disc reflected forward ; ex, exhalant pallial siphon ; g, gill ; go, gonad ; i, intestine ; in, inhalant pallial siphon ; k, kidney ; oe, oesophagus ; p, penis ; pg, pallial genital duct ; pr, prostate ; rcp, right cerebral and pleural ganglia ; rg, repugnatorial gland ; rm, retractor muscle ; spg, supra-oesophageal ganglion ; sr, retracted siphon of cephalic disc ; st, stomach.

Anteriorly a deep groove separates the head lobes from the foot. The mouth opens to it in a median position (m) and on the right the penial sheath. Laterally the cephalic disc and foot (f) merge into one another without obvious boundary. As the mollusc makes its way through the sand the broad head lobes and underlying foot push aside the particles with the action of a snow plough, often with their antero-lateral corners strongly recurved (Fig. 1).

The mantle cavity is deep with a large anterior opening which, however, differs from that of a prosobranch in that it is twisted to the right. The mantle is produced into an inhalant siphon lining the siphonal canal of the shell and a short exhalant siphon on the right (in, ex, Fig. 3). The heart (au, ve, Figs. 2, 3), which can be seen in the roof of the cavity posteriorly, is prosobranch with the auricle in front of the ventricle, and the position of the pallial genital duct (pg) is prosobranch in that it is not sunk into the haemocoel (Fig. 5), and is accompanied by the rectum to near the mouth of the cavity where they open side by side. They both project from the floor of the cavity on the right. The disposition of the remaining organs associated with the mantle cavity conforms to the tectibranch plan, though in some respects they are unusual. The gill is reduced to a simple fold of tissue hanging from the mantle skirt. Its posterior attachment, as in other tectibranchs, is to the right of the genital duct whence it passes towards the left and forwards (g, Figs. 2, 3, 5). Immediately above it and extending as far as its anterior tip, is the kidney (k, lk), an elongated tube with the lumen not subdivided by septa, which appears to run in the axis of the gill and be bathed in the same flow of blood. The kidney lies alongside the posterior part of the gill in *Acteon*, but owing to the reduction of this in *Ringicula* it penetrates further forward and the anterior part of the efferent branchial vessel borders its left wall (epv, Fig. 3).

The gill of tectibranchs is typically a sheet of tissue attached for a proximal part of its length by the two longitudinal margins where the afferent and efferent blood sinuses run. The efferent attachment is near the left limit of the mantle cavity and the afferent arises in the vicinity of the rectum. The first of these is lost in *Ringicula*. The gill is typically folded transversely and the resulting corrugations so deep that they project alternately on either side of the axis and produce a bipectinate appearance. Again this increase in surface does not occur in *R. buccinea*. The opening of the kidney in this species is immediately to the left of the anterior tip of the gill ; it occupies a corresponding though more posterior position in *Acteon*, *Haminea* and other tectibranchs (Guiart, 1901). The left or prebranchial region of the mantle cavity is restricted in size. At the base of the inhalant siphon is an osphradium and posteriorly in the mantle skirt is the bursa copulatrix (bc, Figs. 2, 3, 5) in a position which it occupies in related genera. The postbranchial region is larger and its extreme right border is occupied not by the genital duct and rectum, as in a prosobranch, but by a pronounced exhalant channel which leads to the exhalant siphon (ex, Fig. 3). Two longitudinal ciliated bands, one ventral, parallel to the rectum and accompanied by a conspicuous blood sinus, and the other dorsal and parallel with the first, border the exhalant channel, and the hypobranchial gland lies between the two (db, vb, hy, Figs. 3, 5). The gland is colourless as in other primitive tectibranchs (Fretter & Graham, 1961) and comprises a single layer of secreting cells. Its walls are not folded to increase the secreting area. In the vessels associated with the ciliated bands there are often blood cells packed with granules and they can be traced between the ciliated epithelial cells as though waste was being transported to the exhalant channel. The ciliated bands compensate for the poor ciliation and

small size of the gill for they are responsible for the maintenance of the current of water through the mantle cavity. No exogyrous caecum is developed.

ALIMENTARY SYSTEM

The mouth leads into an oral tube which at its anterior end has a small papilla on each side with the openings of ducts from oral glands, and posterior to these in a ventrolateral position are two prominent bulges. They are raptorial jaws which comprise muscular projections covered with a

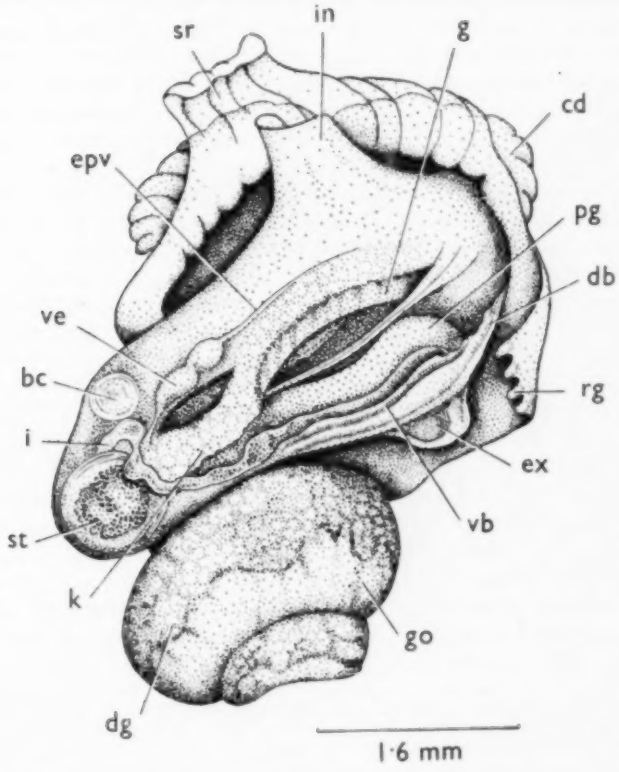

Fig. 3.—*Ringicula buccinea* : whole animal, shell removed, seen from above. Fixed in Bouin, cleared in cedarwood oil.

db, dorsal ciliated band ; epv, efferent pallial sinus ; vb, ventral ciliated band ; ve, ventricle. Other letters as in Fig. 2.

cuticularized epithelium bearing rows of sharp denticles, and can be passed through the mouth to grasp the prey. Interstitial copepods have been seen to be ingested and sometimes Foraminifera are found in the gut. Foraminiferans are the only food mentioned by Pelseneer for *R. conformis*. Within the buccal cavity is the small odontophore which bears transverse rows of hook-shaped teeth and has a deep longitudinal groove mid-dorsally in the absence of median

or rachidian teeth. It is similar to the radula of *Scaphander* and *Philine* (Pruvot-Fol, 1954). There are no radular cartilages. The teeth have been described by Bergh (1904–8) for *R. arctata* and they have been seen in action in *R. buccinea* pulling copepods captured by the jaws into the gut. A ciliated salivary duct opens on either side of the odontophore, leading from a short tubular gland in which the majority of cells give a positive reaction for mucus with toluidine blue. Dorsal to the opening there are numerous glands in the wall of the buccal cavity. The oesophagus has neither the glandular equipment of a prosobranch nor the gizzard plates characteristic of many tectibranchs

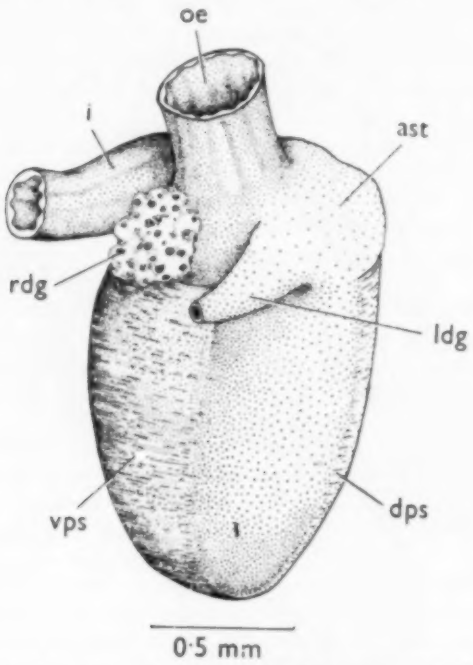

Fig. 4.—*Ringicula buccinea* : stomach and associated structures. Left ventrolateral view. ast, anterior chamber of stomach ; dps, dorsal plate of posterior chamber of stomach ; i, intestine ; ldg, duct of left lobe of digestive gland ; oe, oesophagus ; rdg, small lobe of digestive gland ; vps, ventral plate of posterior chamber of stomach.

for it is a simple tube with a thick muscular coat, lined by a ciliated columnar epithelium which has gland cells. The posterior part of the tube is enlarged and its walls when contracted are folded longitudinally ; this is a characteristic of other tectibranchs and basommatophoran pulmonates (Heidermanns, 1924). It opens to the anterior wall of the stomach (oe, Fig. 4). On structural and functional bases the stomach is divisible into anterior and posterior chambers. The anterior (ast) is ciliated and has the openings of the oesophagus, intestine (i) and two ducts of the digestive gland. The posterior chamber is cuticularized and over its dorsal and ventral walls the musculature is extremely

thick forming crushing plates (dps, vps). This second chamber contains recently ingested food undergoing trituration : here entire copepods and Foraminifera have been found, together with crushed remains, and also numbers of sand grains which will aid in the grinding of the food. In all animals which have been sectioned and dissected the anterior chamber is devoid of such contents and it appears to be merely the passage-way to and from the various regions of the alimentary canal.

The ducts of the digestive gland are of unequal size. The left (ldg) is the larger and from its origin it passes posteriorly between the ventral plate of the stomach and the columellar muscle to the main lobe of the gland which with the gonad comprises the visceral coils. The second duct communicates with the ventral wall of the stomach posterior to the oesophageal opening and leads to an exceedingly small lobe of the gland (rdg) which lies against the pallial genital duct. Some cells of the digestive epithelium are conspicuous owing to their dark brown inclusions. They are excretory cells similar to those which have been described for *Acteon* (Fretter, 1939), and the histology of the rest of the gland is similar to that of this tectibranch. The intestine arises not far from the left duct of the digestive gland and then curves around the posterior wall of the pallial genital duct and runs alongside it to open at the base of the exhalant siphon (i, Figs. 2, 3). Its broadest part is at its origin. The intestine is ciliated throughout.

REPRODUCTIVE SYSTEM

The hermaphrodite gland of *R. buccinea* comprises a central spermatogenous sac surrounded by the female acini which open into the sac. This is a more advanced condition of the gland than in the majority of tectibranchs in which the two kinds of genital products are developed side by side. Ripe sperm are stored in the gonadial or little hermaphrodite duct. It passes forward above the columellar muscle to the posterior end of the mantle cavity (gd, Fig. 5), curves around the left wall of the initial part of the pallial genital duct and opens into it dorsally. The duct of the receptaculum seminis, a rather elongated sac (rs), runs parallel with the terminal part of the gonadial duct and opens into the pallial duct alongside it. They enter a chamber which on account of its position and the structures associated with it will be called the fertilization chamber. It is lined by a ciliated epithelium and embedded in the albumen gland into which it opens. The walls of this gland are thin and deeply folded and the resulting lobes are closely packed against one another ; the glands form a single layer of tall columnar cells. Pelseneer (1925) stated that in *R. conformis* the hermaphrodite duct soon bifurcates after leaving the gonad to give oviduct and vas deferens. I have been unable to trace this in *R. buccinea* in which it would appear that the pallial duct is hermaphrodite, with the vas deferens as a ciliated groove constricted somewhat from the glandular oviduct. The region of this duct anterior to the albumen gland which is homologous with the mucous gland of other tectibranchs, is a straight tube with a deep and complex fold subdividing its lumen especially posteriorly (f). The ciliated groove (vd) runs alongside the base of the fold. The epithelium of the gland is composed of tall secreting cells and wedge-shaped

ciliated cells. The anterior region of the oviduct is a vagina into which opens the narrow muscular duct from the bursa copulatrix (bc, Figs. 2, 3, 5). In some individuals which have been sectioned the duct is distended with spermatozoa and the pouch has secretions and only a few sperm. The staining reactions of the secretions suggest that they are derived from the mucous and prostate glands and if this is their origin then presumably the pouch, as in other tectibranchs, is no longer the main depository for the seminal fluid, but for the waste material from the reproductive ducts (Lloyd, 1952).

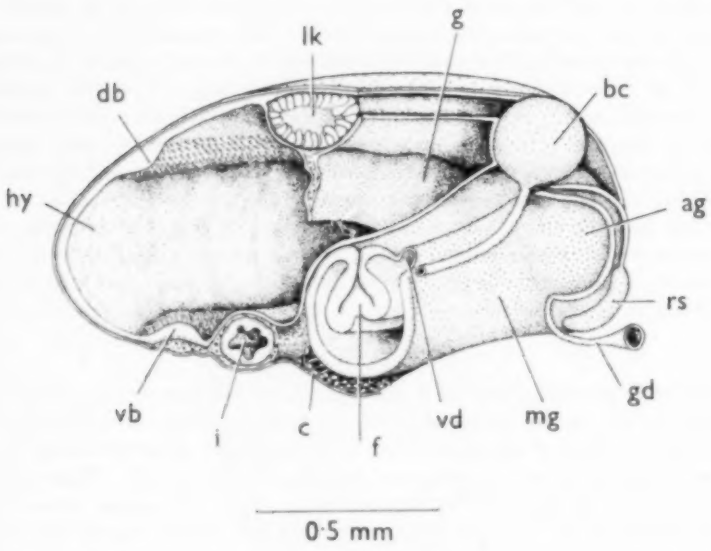

Fig. 5.—*Ringicula buccinea* : diagrammatic representation of structures associated with the posterior region of the mantle cavity. The heart and afferent branchial vessel have been omitted and structures at the posterior end of the genital duct somewhat displaced.
ag, albumen gland ; bc, bursa copulatrix ; c, columellar muscle ; db, dorsal ciliated band ; f, fold projecting into lumen of mucous gland ; g, gill ; gd, gonadial duct ; hy, hypobranchial gland ; i, intestine ; lk, lumen of kidney ; mg, mucous gland ; rs, receptaculum seminis ; vb, ventral ciliated band with underlying blood sinus ; vd, vas deferens.

It is characteristic of most tectibranchs that a seminal groove leads from the open vas deferens at the common genital aperture to the penis on the head, though in some (e.g. *Acteon*, *Hydatina*) this cephalic vas deferens is a duct. I am unable to trace either duct or seminal groove in this region in *R. buccinea*. The cephalic disc seals off the mantle cavity and the genital aperture when the animal is creeping, though it may be turned forward at copulation : even then the course of a seminal groove from genital aperture to penial sheath would be circuitous. An inconspicuous groove may have been overlooked in so small an animal and it may be obvious only at the time of copulation.

The retracted penis and the prostate gland open to the penial sheath which is lined by a ciliated epithelium. Both penis and prostate (p, pr, Fig. 2) are tubular structures projecting into the haemocoel alongside the oesophagus ; the prostate is the broader and longer. It would appear that in Pelseneer's figures of sections of *R. conformis* the penis is labelled sperm duct. Indeed it has the appearance of a duct for there are no blood spaces in its walls and it is lined by a ciliated epithelium which is surrounded by a thick coat of circular muscles. Gland cells surround the muscles, their ducts passing between the fibres to open between the ciliated cells. In one specimen which was sectioned the penis was partially protruded so that its tip projected from the surface of the body and at its base was the prominent papilla on which the prostate opens. In the epithelium of this gland secreting cells alternate with ciliated cells and a criss-cross of muscle fibres surrounds the epithelium. Copulation has not been observed so that the method by which sperm enter the penis and are transferred to another individual is unknown.

NERVOUS SYSTEM

The nervous system is prosobranch in its streptoneury and lack of fusion of the ganglia, but opisthobranch in having a long pedal commissure. The ganglia in each half of the nerve ring which surrounds the oesophagus are closely apposed to one another. The boundary between them is obvious since muscle fibres surround the short connectives. The suboesophageal ganglion is the only one on the visceral loop which has migrated forwards. It is applied to the left pleural giving four ganglia in this half of the ring—cerebral, pedal, pleural and suboesophageal. The supraoesophageal ganglion (spg, Fig. 2), on the long supraoesophageal connective, is near the osphradium and the visceral ganglion against the median wall of the pallial genital duct. Well developed buccal ganglia are in the usual position at the level of the nerve ring.

DISCUSSION

Boettger (1954), considering the relationships of euthyneurous gastropods, placed the Ringiculidae on an independent line of evolution arising from the Acteonidae. He regarded them as closer to the Basommatophora than other tectibranchs and he thought of the basommatophorans as arising from an acteonid stock. The present study of *R. buccinea* supports these conclusions concerning the Ringiculidae.

Ringicula is the type of opisthobranch in which the body can be fully retracted into the shell and a large part of the shell, which has a well developed spire, is exposed when the snail is fully extended. The habit of burrowing is shared with other tectibranchs like *Acteon*, *Scaphander*, *Philine* and *Haminea*, and associated with this is the development of a head shield and the withdrawal of the eyes from the surface. In *Ringicula* the head shield is a sheet of tissue which can be turned back over the shell, and together with the foot it shovels away the sand during burrowing. It thus resembles the flattened cephalic tentacles of *Acteon* but unlike these is fused laterally with the foot so that together they envelop the shell anteriorly ; mid-dorsally it is produced into an inhalant siphon which is a special feature characteristic of the family

Ringiculidae. The siphon retains contact with the surface during burrowing and avoids by its movement the inspiration of particles which in so small an animal might be harmful.

In other tectibranchs in which the visceral mass is large, coiled and covered by a shell an exogyrous caecum is developed, providing an additional respiratory surface and leading a current of water to the neighbourhood of the visceral hump. It may be associated with the less efficient gill of the opisthobranch as compared with the prosobranch. Its absence in *Ringicula* is perhaps correlated with the small size of the snail giving a comparatively larger surface area exposed to the water. The specialized part of the mantle from which an exogyrous caecum may be produced is nevertheless one of the obvious tectibranch features, comprising two longitudinal ciliated bands along the exhalant channel from the mantle cavity and a glandular area between. The exhalant channel and not the gill is responsible for driving water through the mantle cavity, and this may also partly hold for the larger tectibranchs in which the gill is not reduced and the mantle cavity is deep. The opening of the mantle cavity is directed forwards and to the right—a reorientation from the prosobranch condition which indicates the early stages of detorsion, though this has not affected the streptoneurous nervous system. The heart is prosobranch with the auricle in front of the ventricle, but like the heart of other tectibranchs it lies in the thickness of the mantle skirt. The disposition of the rest of the organs associated with the mantle cavity is typically tectibranch : the kidney is in the mantle skirt and opens far forwards ; the afferent branchial vessel arises directly from the perirectal sinus ; there is no penis in the mantle cavity for it is withdrawn into a sheath when not in use and projects into the haemocoel ; the genital duct lies in the floor of the mantle cavity with the exhalant channel to its right.

The rotation of the mantle cavity to the right as compared with its forward position in prosobranchs must involve some differential growth in the right and left halves of the mantle skirt (Fretter & Graham, 1961). A continuation of the same process which may have been responsible for bringing the rectum from its median position in the Diotocardia to the right side of the mantle cavity in the Monotocardia, may cause it to migrate still further until with the genital duct it comes to lie on the floor of the mantle cavity with the exhalant channel to the right. This results in the genital duct retaining its position with respect to the cephalic penis which is not involved in detorsion. On the other hand Perrier & Fischer (1911) regarded the ventral position of the rectum and genital duct as being brought about by an incorporation of the original right lateral wall of the mantle cavity in its floor, accompanying a depression of the cavity and an expansion of the head foot. It seems likely that both processes are involved to some extent. The orientation of the organs at the posterior end of the mantle cavity of *Ringicula* suggests that the process of detorsion here has proceeded further than anteriorly. Thus the gill crosses the genital duct and lies on its right side, the kidney accompanying it. This appearance may be related to the fact that the genital duct and rectum have become anchored to the floor of the mantle cavity in the incorporation of the right half of the mantle skirt as suggested by Perrier & Fischer,

whereas the structures of the left half of the skirt are free to change their relative position. The shallowing of the mantle cavity in tectibranchs as compared with the prosobranchs may be correlated with the less effective gill with its weaker ciliation and smaller surface area, which is compensated for by the increased cephalic and pedal sites of possible respiratory exchange.

The rectum in *Ringicula* is long bringing the anus far forwards, whereas it is more typical of related tectibranchs for it to open deeper within the mantle cavity and the faeces to be carried to the opening in the strong exhalant flow of water.

Like other opisthobranchs *Ringicula* has special glands associated with the exposed parts of the body. They are conspicuous multicellular structures surrounded by a thick coat of muscle fibres which expels the secretion with some force when the animal is irritated. The secretion is toxic to small animals. Similar repugnatorial glands have been described for the tectibranchs *Acteon* and *Onchidella* and the aquatic pulmonate *Siphonaria* (Fretter& Graham, 1954). This is not the only resemblance in external features to the pulmonate *Siphonaria* which is classified near the base of the basommatophoran line of evolution (Boettger, 1954), for it has a similar exhalant channel from the mantle cavity which is bordered by dorsal and ventral ciliated bands and has an identical relationship with the other pallial organs (Hubendick, 1945) ; there is no exogyrous caecum ; the kidney spreads through the mantle skirt and opens towards the distal end of the gill ; the restricted opening of the mantle cavity is anterior and on the right.

In opisthobranchs and pulmonates the gonad is a hermaphrodite gland with a single connexion to the accessory glands and ducts of the reproductive system. These are homologous with the pallial ducts of prosobranchs though with few exceptions they have separated from the body wall which restricted their further evolution and are freed to the haemocoel. *Ringicula* and *Acteon* are two exceptions for in them the pallial duct retains its connexion with the body wall and has a straight course to the genital aperture. The pallial duct of *R. buccinea* is incompletely subdivided into spermiducal and oviducal parts like *Scaphander* and *Philine* (Lloyd, 1952) ; this is also an opisthobranch character displayed by *Siphonaria* (Cottrell, 1911). Again, as in *Scaphander* and *Philine*, there are two sperm pouches associated with the duct, a receptaculum at the upper end and a bursa which communicates with the vagina by a long duct. The walls of the pallial oviduct are deeply folded with an epithelium of gland cells and ciliated cells, but unlike more advanced tectibranchs they show no complexity of outgrowths into the haemocoel.

The replacement of the external penis of the prosobranch by the invaginable penis of the tectibranch seems to have been necessitated by at least two factors, the difficulty of housing an anterior copulatory organ in a mantle cavity which is pushed back to the right, and the awkwardness of an unhoused penis in an anterior situation in a burrowing animal. The tubular prostate alongside the penis is also a character shared with the related tectibranchs *Scaphander* and *Philine*.

These tectibranchs have a triturating region of the oesophagus in which the food is crushed for it is often of such a form or size that it cannot undergo

a preliminary fragmentation by the radula. The oesophagus also provides a roomy chamber, the crop, in which food can be mixed with digestive enzymes from the digestive gland (Fretter, 1939). Oesophageal plates are absent in *Ringicula* (and *Acteon*) and the oesophagus appears to be merely a conducting tube from mouth to stomach. The triturating chamber is the enlarged posterior part of the stomach which as in some basommatophorans and in the aberrant opisthobranch *Onchidella celtica* (Fretter, 1943) is muscular and cuticularized (Heidermanns, 1924). This region is large in *Acteon* but the thinness of its walls suggests that the food of this mollusc needs less treatment prior to digestion. The anterior chamber of the stomach shows the opisthobranch tendency of having oesophageal and intestinal openings and the liver ducts close together, and this is the only part of the stomach represented in more advanced tectibranchs (Graham, 1949).

The possession of labial glands, the small size of the salivary glands, the use of the radula for grasping rather than fragmenting the food, the uniformity of the radular teeth, the lack of oesophageal glands, the elaborate histology of the digestive gland and columellar teeth are all opisthobranch characters. The nervous system with its streptoneury and lack of fusion of ganglia is prosobranch in plan.

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SOME FEATURES OF THE VASCULARIZATION OF THE HYPOTHALAMUS AND PITUITARY STALK IN THE MINNOW *PHOXINUS PHOXINUS* L.

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(With 1 plate and 1 figure in the text)

An account is given of the vascularization of the pituitary stalk and of the associated region of the hypothalamus in the minnow. It is pointed out that, making allowance for the fact that the teleosts are widely separated from the main line of vertebrate ascent, the pattern of this vascularization has something in common with that of a median eminence. A particular feature is the existence of a capillary bed in the floor of the infundibular recess and this is shown to have a close topographical relationship with cells containing granules which are intensely stained by chrome-alum-haematoxylin. These is some evidence that these may be secretory cells and that their products pass into the blood stream and into the third ventricle.

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INTRODUCTION

A great deal of attention has recently been focused on the problem of the relationship of the pituitary gland with the central nervous system in the higher vertebrates, but the fish remain largely unexplored from this point of view. The significance of the median eminence and of its associated portal system as a factor in the neural control of adenohypophysial function has been extensively argued (Harris, 1955), particularly with reference to birds and mammals, but it has been supposed that these features are substantially a characteristic of the tetrapods and that an eminence is either absent from teleost fish or at most represented in a general way by the entire neurohypophysis (Green, 1951). It would, however, be surprising if a structure so characteristic of higher vertebrates were wholly absent from a major group of fish, particularly so if its function in endocrine regulation is of the central importance which has been claimed for it. Moreover, the description of a rudimentary eminence in the dipnoan fish *Protopterus* (Wingstrand, 1956) and indications of one in the cyclostome *Myxine* (Olsson, 1959) suggest that the situation in other groups of fish would bear re-examination. It is from this point of view, therefore, that the present paper provides a description of

some features of the floor of the hypothalamus of the minnow, although it will be appreciated that since the teleosts are remote from the main line of vertebrate ascent any interpretation of this region must be very tentative in the present state of our knowledge.

MATERIAL AND METHODS

The animals were obtained in part from Lake Windermere, through the kind cooperation of the staff of the Laboratory of the Freshwater Biological Station, and in part by collecting at a site in Oxfordshire. Fixation was usually in mercuric formol (sat. sol. of mercuric chloride 9 parts, formol 1 part), and was followed by decalcification in a mixture of nitric acid (5 ml.), formaldehyde (5 ml.) and 70 per cent alcohol (90 ml.), and routine embedding in wax. Transverse and longitudinal sections of the pituitary and floor of the brain were stained by the Azan procedure and with Gomori's chrome-alum-haematoxylin and phloxin, and some use was also made of fixation in Bouin's fluid followed by staining with Harris's haematoxylin and eosin.

OBSERVATIONS

The pituitary of the minnow (Kerr, 1942) is clearly divisible into an adenohypophysis and a neurohypophysis, these two components being closely interdigitated as is usual in teleosts. The neurohypophysis is connected by a short stalk at its anterior end with the floor of the diencephalon (Fig. 1), and towards this point the third ventricle extends ventrally in the middle line as the infundibular recess (Pl. 1, figs. 1 & 3), stopping short, however, of the stalk itself, which is thus solid. The ventricle is lined by ependymal cells which are rather densely staining, pyramidal in shape, and regularly arranged at right angles to the lumen. The rest of the cells in the floor of the diencephalon possess large granular nuclei, each with a prominent nucleolus, while the cell bodies are drawn out into thin fibrils ; they thus build up a loose-textured tissue, which is continued down the stalk into the neurohypophysis.

A conspicuous feature of the stalk is the hypothalamo-hypophysial tract with its chrome-alum-haematoxylin-positive nerve fibres. This tract has not been specially studied in this work, but it has been assumed that, as in other teleosts (Hild, 1950) it is a neurosecretory pathway from the nucleus preopticus, which is well developed at the anterior end of the diencephalon. An additional hypothalamic nucleus, the nucleus lateralis tuberis, seems to be a common feature of many teleosts, but is known to be absent in the minnow. There is evidence, however, of another type of differentiation in the floor of the infundibular recess, for certain cells contain well-defined chrome-alum-, haematoxylin-positive granules. These cells (Pl. 1, fig. 3) are scattered through the floor of the diencephalon in a clearly defined region (Fig. 1), lying above the pituitary stalk, and extending from the level of the posterior edge of the latter up towards the third ventricle immediately anterior to the stalk. Their granules lie in the cytoplasm, usually in the more peripheral part of the cell body but sometimes around the nucleus, and examination of a large number of fish shows that they vary both in size and abundance. In some animals they may be quite inconspicuous, but in many they are numerous and easily

seen, and it must be emphasized that they are always quite distinct from the chrome-alum-haematoxylin-positive material in the nerve fibres of the hypothalamo-hypophysial tract, being situated for the most part dorsal and posterior to them.

Associated with these cells is a very characteristic pattern of vascularization. Although it has sometimes been said that blood leaves the pituitary gland of teleosts through the stalk (e.g. Florentin, 1936), the more recent and acceptable view is that it passes down the stalk (e.g. Kerr, 1942) and is drained into venous channels at the anterior and posterior ends of the gland. In the minnow this blood is largely derived from the internal carotid arteries through a median vessel which arises from them at the level of the anterior edge of the optic chiasma. This vessel, which can be conveniently referred to as the ventral pituitary artery, passes through the chiasma and runs to the pituitary along the ventral floor of the brain within the meningeal membranes. As it approaches the gland (Fig. 1, *vpa*) it divides and forms around the base of the stalk an intrameningeal ring vessel (Fig. 1 and Pl. 1, fig. 2, *rv*) such as has been noted by Florentin (1936) in cyprinids and salmonids ; from this ring branches

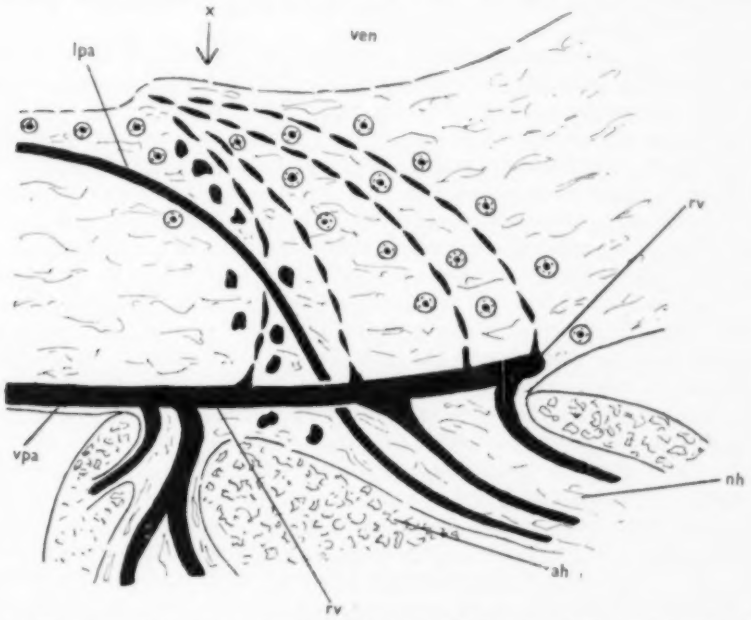

Fig. 1.—Diagrammatic reconstruction to illustrate certain features of the organization of the pituitary stalk and of the adjacent region of the floor of the brain in the minnow. The distribution of the granular cells is indicated by dotted circles. Blood corpuscles in the capillary bed are represented as elongated black bodies, and those drained down into the pituitary stalk as irregular black ones. For further explanation see text.
ah., adenohypophysial tissue ; *lpa.*, lateral pituitary artery ; *nh.*, neurohypophysial tissue ; *rv.*, ring vessel ; *ven.*, third ventricle ; *vpa.*, ventral pituitary artery ; *x*, approximate level of the transverse sections shown in Pl. 1, figs. 1 & 2.

pass down into the gland and give rise to the rich vascularization of the neurohypophysis, this in its turn vascularizing the adenohypophysis.

Towards the anterior end of the third ventricle there can often be distinguished a conspicuous unpaired vessel which runs down one side of the diencephalon and then backwards through its floor to pass down the centre of the pituitary stalk and into the gland, where it merges with the vessels derived from the ventral pituitary artery. It is convenient to refer to this unpaired vessel as the lateral pituitary artery (Fig. 1, *lpa*), but it is difficult to judge whether it is of much functional importance, for while in some specimens it is very clearly defined, in others it is impossible to detect. It arises from an artery which runs forwards along the roof of the third ventricle and which is itself derived from the internal carotid arteries. This dorsal artery takes blood to the anterior region of the diencephalon, including the nucleus preopticus, and also gives off small branches which vascularize the ventro-lateral walls of the diencephalon. The lateral pituitary artery is probably to be interpreted as one of these branches which has become enlarged in relation to the outgrowth of the neurohypophysis from the floor of the diencephalon, and it may well be that its degree of development varies in different individuals.

A final and important feature is a region of vascularization in the floor of the infundibular recess immediately above the stalk. In many specimens it is quite inconspicuous and could be overlooked, although scattered blood corpuscles can almost always be seen, but in others it is congested with blood and is then so conspicuous in sections as to suggest at once that some special physiological importance attaches to this region. It is significant, therefore, that in transverse sections it forms a well-defined arc (Pl. 1, figs. 1 & 2) overlying the pituitary stalk and extending up to the lining of the third ventricle, while in transverse and longitudinal sections it can be seen that its distribution conforms closely with that of the granular cells already described (Fig. 1).

The lateral pituitary artery runs through, or very close to, this region and it is quite possible that some of the blood in the latter could be derived from it or from the smaller vessels of the brain wall, but it is difficult to be sure of this. What is certain, however, is that much of this blood lies in capillaries which are directly connected with the ring vessel by many small offshoots which extend upwards and inwards from the latter (Pl. 1, fig. 2). Thus in transverse sections a capillary bed extends as a continuous arc from one side of the ring vessel to the other, and it seems evident that it must be traversed by blood from the ventral pituitary artery. In those animals in which the bed is richly vascularized it can clearly be seen that blood is forced upwards and forwards towards the third ventricle, and it seems likely that some of it must diffuse into tissue spaces, for the capillary walls are not always distinguishable, particularly in the more central region. Under these circumstances a tongue of tissue and blood corpuscles may project into the ventricle, but such an appearance is not found in animals in which the vascularization is less intense, and it appears, therefore, to be a result of the effect of blood pressure and congestion, possibly exaggerated by artifacts of killing and fixation. However, in most animals it is possible to see blood corpuscles lying

close against the lumen of the infundibular recess, and one may assume that the normal flow of the blood must bring it into close relations with the latter.

Since it is not possible to study the course of the circulation by direct observation one can only infer the route which it must follow. There seems no reason why some of the blood traversing the capillaries should not pass from one side of the ring vessel to the other, since vessels can clearly be seen to extend across the middle line in transverse section, but another route is possible, for there are good indications of the drainage of blood down into the stalk, probably through tissue spaces rather than through capillaries (Fig. 1 and Pl. 1, figs. 1 & 2). In the upper part of the stalk the fibres of the hypothalamo-hypophyseal tract separate into two groups lying left and right of the middle line, and blood corpuscles can be traced down through the space left between these groups. Such corpuscles cease to be distinguishable in the pituitary itself as a separate flow, and they presumably merge with the rest of the pituitary blood supply.

Returning now to the granule cells, the distribution of these agrees so closely with that of the capillary bed that it seems reasonably certain that there must be some functional relationship between the two. The fact that granules are present within the cells is not conclusive evidence that this relationship is a secretory one, but it is significant that granular material closely resembling them can easily be seen in favourable preparations lying around the neighbouring erythrocytes, either within the capillaries or in the tissue spaces (Pl. 1, figs. 3 & 4). The possibility that such material might have been derived from the haematoxylin-stained contents of the neurosecretory fibres in the diencephalon floor and pituitary stalk must be borne in mind, but such a source is actually quite unlikely, since, apart from the close resemblance of the granules to those in the granule cells, they are only found in the capillaries adjacent to them and seem never to occur in those which run close to the fibres.

It seems possible, then, that the granules may well be a secretory product, and the associated vascularization would then provide a means by which this could be transmitted to the third ventricle. This is most clearly demonstrated in those animals, already mentioned, in which the vascularization is intense and the tongue of tissue projects into the lumen, for a dense mass of secretory granules is associated with the erythrocytes in the tongue, and is visible also in the lumen. Such a distribution, in fact, may be regarded as confirmatory of the above analysis of the course of the circulation, particularly since there is no sign of the association of granules with corpuscles in the lateral pituitary vessel or in the other small vessels which, according to that analysis, are bringing blood down towards the secretory region.

It is difficult to determine whether the secretion passes in any other direction than into the third ventricle. It has been suggested above that the blood from the capillary bed may pass back into the ring vessel or drain down the stalk, but both of these paths are difficult to study in chrome-alum-haematoxylin preparations. Some positive coloration can be made out in the ring vessel and also in association with some of the corpuscles in the stalk, but the significance of this is uncertain since haematoxylin-stained connective

tissue fibres occur in the wall of the vessel while the scattered corpuscles are so close to the neuro-secretory fibres in the stalk that any material associated with them might well be derived from the latter. What is certain is that secretory granules are only readily identifiable in the capillaries running towards or near the third ventricle, so that the latter seems likely to be the main route for their passage. Occasionally, however, one can recognize in the anterior region of the neurohypophysis a few granules cells exactly similar to those found in the main centre above the stalk, as is quite understandable, for the neurohypophysis is a direct extension of the floor of the infundibular recess and closely resembles it in general appearance. It follows that the possibility of a direct functional relationship between the granular secretion and the pituitary is certainly not excluded.

DISCUSSION

The adenohypophysis of higher vertebrates has a vascularization distinct from that of the neural lobe, its blood passing first through a capillary bed in the median eminence and then through portal vessels to the glandular tissue. Green (1951) has defined the median eminence as that part of the neurohypophysis which receives blood from this hypophysial portal circulation, or which has a common vascularization with the adenohypophysis, and, using the latter criterion, has suggested that in teleosts it may be represented by the whole of the neurohypophysis. It has been argued in recent years that the median eminence is concerned with the relaying of instructions to the adenohypophysis by means of chemical transmitters discharged into the portal vessels, and originating either in the neurosecretion of one or other of the hypothalamic centres or perhaps in the glandular zone of the eminence itself. The possibility that nerve fibres in the neurohypophysis of teleosts may be concerned in the regulation of adenohypophysial function certainly merits serious consideration (Barrington, 1960 ; Wingstrand, 1959), but the present work seems to show that, quite apart from this, the pattern of neurohypophysial organization in the teleosts may be even closer to that of higher forms than has previously been recognized.

The median eminence in *Rana* (Green, 1947) receives its blood from a hypophysial artery running in the meningeal membranes ; this seems directly comparable with the ventral pituitary artery of the minnow, and it would appear logical to homologize the capillary bed in the diencephalon of the latter with that of the median eminence of the former, for it lies in the same morphological position and receives its blood from a similar source. The resemblance is not an exact one, nor can it be expected to be, for, as emphasized above, the teleosts are not on the main line of ascent to higher vertebrates, and must necessarily have developed their own structural and functional specialisations, but one may reasonably look for similarities in the basic features of organization in the two lines. So also, in comparing the conditions in the minnow with those in *Lepidosiren* as described by Wingstrand (1956), the indentation of the ventral surface of the infundibulum by capillaries in the latter bears a suggestive resemblance to the much more extensive development of capillaries from the ring vessel of the former. One cannot, of course, claim that there is a true portal system associated with the pituitary in the minnow,

and it seems clear that much of the blood in the ventral pituitary artery enters the gland direct without circulating through the capillary bed, but the fact that some can certainly be deflected through the latter suggests a pattern of vascularization not wholly dissimilar from that of higher forms. In any case, the degree of development of a portal system must reflect the distance which the blood has to traverse, and in the minnow this is probably too short to make such a development necessary.

Secretory activity in the diencephalon of fish has hitherto been attributed to neurosecretory cells of the nucleus preopticus and also of the nucleus lateralis tuberis in those fish which possess this. It is suggested here, however, that the granule cells of the minnow may be indicative of secretory activity associated with the specialized vascularization of the floor of the infundibular recess. If this is so, and the evidence is certainly not yet complete, we should be dealing with activity of a character different from that of the neurosecretory centres, since the cells concerned are clearly not neurones. It is of interest, however, that their product seems to be conveyed mainly into the third ventricle, for certain cells in the nucleus preopticus of the Anura (Bargmann, Hild, Ortmann & Schiebler, 1950) and of the tench (Hild, 1950) discharge their secretion into that cavity, as also do the cells of the nucleus tuberis of the latter animal (Hild, 1950). The significance of such details is at present hard to evaluate, and the immediate need is to determine to what extent other fish show a pattern of organization similar to that found in the minnow. That the situation is unlikely to be peculiar to the latter is indicated by Bretschneider and de Wit's (1947) reference to the presence of a vascular network close to the pituitary stalk of the teleost *Rhodeus amarus*, a feature for which they were not able to suggest an explanation.

It may be concluded that the vascularization of the floor of the infundibular recess in the minnow presents some features suggestive of a resemblance to the median eminence of higher vertebrates, and that these are associated with indications of secretory activity. Wingstrand (1959) has discussed the implications of the probability that the eminence and the neural lobe have evolved from a common neurohypophysis in a fish-like ancestor, and conditions in the minnow certainly conform with such an interpretation, for its neurohypophysis is a simple extension of the infundibular floor and occasionally contains granule cells identical with those described here as characterizing the vascular zone of the latter. The functional interpretation of the situation is, however, quite obscure. There is certainly a great deal of variation in the conditions of the granule cells and in the intensity of vascularization of the capillary bed. Such variation gives the impression of reflecting fluctuations in the activity of this region, but until this aspect has been thoroughly examined, and the situation explored in other fish, it does not seem profitable to press the discussion further.

ACKNOWLEDGMENT

I am indebted to Miss J. M. Plumtree (Mrs J. M. Matty) for skilful technical assistance and for cooperation in the interpretation of the blood supply of the pituitary.

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EXPLANATION OF PLATE

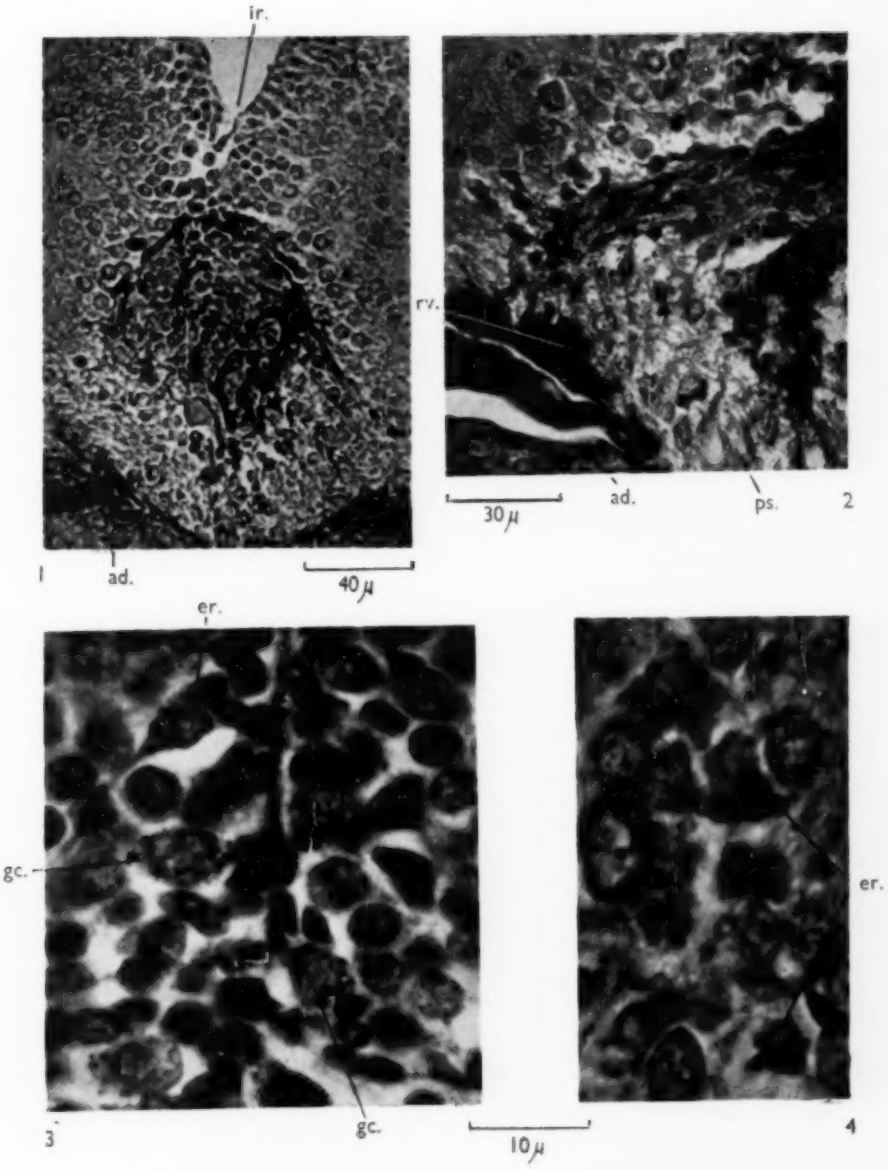
Fig. 1.—Transverse section (Azan stain) across the floor of the diencephalon in the minnow to show the region of intense vascularization (black in the photograph) lying between the infundibular recess (top centre) and the pituitary stalk (extreme bottom centre). The approximate level of this section and that shown in the next photograph is indicated by the guide line *x* in Text-fig. 1.

„ 2.—Transverse section (Azan stain) at a higher magnification across the left half of the same region as is shown in the previous figure, but from another animal. Note that to the left the capillary system is connected with the ring vessel and that from the mid-point of the capillary arc (at the extreme right of the field) there is a drainage of blood downwards towards the pituitary stalk.

„ 3.—Granular cells in the floor of the infundibular recess of the minnow. Note at the upper left of the field that material similar to the contents of these cells is closely associated with an erythrocyte and appears to lie within the capillary which extends away to the left. The line passing vertically down through the middle of the field is the ventral extension of the infundibular recess with its lumen obliterated. (Chrome-alum-haematoxylin and phloxin.)

„ 4.—An area in the floor of the infundibular recess of the minnow showing a line of erythrocytes extending upwards from the bottom to the top of the field. The dark masses associated with them resemble the contents of the granule cells, although the separate granules here tend to clump together, the effect being exaggerated in photographic reproduction. Capillary walls are not visible. (Chrome-alum-haematoxylin and phloxin.)

ad., adenohypophysis ; *er.*, erythrocyte ; *gc.*, granular cell ; *ir.*, infundibular recess ; *ps.*, pituitary stalk ; *rv.*, ring vessel.



Vascularisation of the hypothalamus and pituitary stalk in the minnow.

THE BREEDING SEASONS OF SLUGS IN GARDENS

BY

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[Accepted 8th March, 1960]

(With 9 figures in the text)

Generalized life cycles of five slug species were ascertained from new data on weights of individual slugs together with information on the seasonal state of their genital organs in conjunction with Barnes & Weil's unpublished data on weights.

Arion hortensis hatches mainly in January and February, grows through the summer months to become mature in September and October. These adults live through the winter, laying eggs and gradually losing weight and die before July of the following year.

The eggs of *Arion subfuscus* are mainly laid in the autumn (late August and September) and hatch sporadically through the winter. The young slugs grow through the spring to become mature in July and the adults die soon after egg-laying.

Agriolimax reticulatus breeds throughout the year but the rate depends on the weather and each year there is a period of intense egg-laying associated with the new spring vegetation, that results in a summer abundance of individuals.

Milax budapestensis hatches during the autumn and winter, grows through the summer to become mature in late October and November when they mate and eggs are laid in the autumn and throughout the winter. The adults die before July of the following year.

Milax sowerbii probably hatches in early spring, grows throughout the summer, becomes mature, mates and starts to lay eggs in September, October and November. The adults die soon after egg-laying.

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INTRODUCTION

There is little precise information about the populations, feeding habits and the breeding seasons of slugs, but Barnes & Weil (1944 & 1945) and Barnes (1946 & 1953) by collecting after dark found that each species reaches its greatest numbers at a particular season each year and the weight of each species in random samples was most soon after numbers were greatest. They suggested that mating was also likely to be most frequent when the slugs are heaviest, but it is important to know whether the mating season is protracted as in *Agriolimax reticulatus* or short as in *Arion subfuscus*.

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Before attempting to assess populations by marking methods, I decided to see if more detailed knowledge concerning the breeding seasons of slugs could be obtained by knowing the state of the genital organs throughout the year. I was fortunate in being able to use the large series of individual weights amassed by Dr Barnes and also the garden of 5 Moreton End Lane, Harpenden, which was the one chiefly used by him.

METHODS

The method of collection was the same as used by Barnes & Weil, and as they stressed, the number found active on any one night does not necessarily represent a fixed proportion of the total population. The number active depends on the weather and is not likely to be the same for each species, but collecting on numerous nights probably ensured that all the slugs appeared on the surface on some occasion and so ran the risk of being collected. Collections were made on damp, still nights when slugs are most active.

The samples were brought into the laboratory next morning, the various species were counted and placed in separate petri dishes. An attempt was made to keep the slugs in 100 per cent RH to prevent any loss in weight. Each individual was weighed in water in a separate tube where it remained alive until it could be dissected. When the sample was large this could not be done for several days.

Each slug was dissected alive and notes made of the condition of the genital organs. Squashes in water and aceto-carmine solution were made of the contents of the spermathecae and hermaphrodite ducts.

It was hoped to place the slugs into four categories : (i) immature, (ii) mature but unmated, (iii) mated but not egg-laying and (iv) egg-laying. The difficulty of interpreting the variations in the physiology of sex development prevented placing the slugs into such clear-cut categories. Only twice were eggs found in the genital ducts, and on each occasion the slugs were actually laying eggs. It was concluded that eggs are not stored before laying, at least not in organs anterior to the albumen gland. Sperm was found in the hermaphrodite duct of nearly all mature slugs, showing that sperm and eggs are shed together from the ovo-testis.

The slugs were therefore placed into three categories according to the following criteria : (i) immature slugs—those with no sperm in the hermaphrodite duct, (ii) mature but unmated slugs—those with sperm in the hermaphrodite duct but with an empty spermatheca, and (iii) mature-mated slugs—those with sperm in the spermatheca and the hermaphrodite duct, and in some species the remains of a spermatophore. In *Arion hortensis*, *A. subfuscus*, *Milax budapestensis* (*gracilis*) and *M. sowerbii* a distinct spermatophore is passed at mating but in *Agriolimax reticulatus* the sperm is passed as a gelatinous ball and therefore no recognizable fragments can be seen in the spermatheca after mating.

Arion hortensis, *Milax budapestensis* and *Agriolimax reticulatus* were studied in this way from September 1957 to December 1958. *Arion subfuscus* and *Milax sowerbii* were studied from May 1958 to December 1958.

ARION HORTENSIS

Barnes & Weil showed that *A. hortensis* was most abundant during October and November and least during June and July, and my results confirmed this. The dissections indicate that in 1958 immature slugs are most numerous over the period May to August, mature-unmated slugs in September and October and mature-mated slugs from February to April (Fig. 1, d, c, b). The average weight for immature and mature slugs was calculated for each sample. Both categories of mature slugs were considered together for this purpose. The average weight of immature slugs is lowest when they are least numerous and

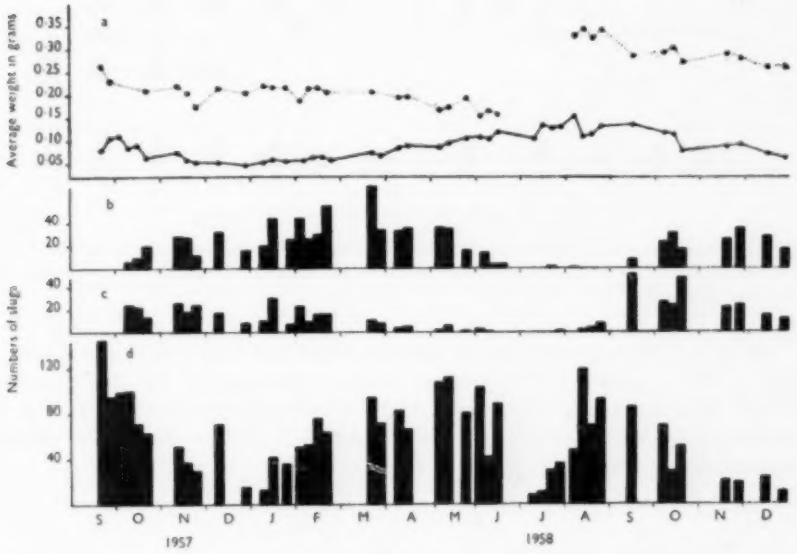

Fig. 1.—*Arion hortensis* : (a) average weight of mature slugs (dotted line), immature slugs (full line) and numbers of (b) mature-mated, (c) mature-unmated, (d) immature slugs collected in 1957 and 1958.

highest when they are most abundant, whereas the average weight of mature slugs is highest when they are least numerous and lowest before they disappear in July. From this it can be inferred that most hatching occurs in January and February, that growth continues during the spring and summer, that maturity is reached in September and that mating takes place throughout the winter and early spring. As the immature slugs reach maturity the average weight of mature slugs increases. It gradually decreases as mating and egg-laying proceeds throughout the autumn, winter and the following spring. Histograms calculated on the percentage weights of the slugs collected per month for the years 1945, 1957 and 1958 illustrate the growth of *Arion hortensis* throughout the year (Fig. 2).

During July few slugs were collected, possibly because of the temperature (Fig. 5 a). I suggest that the immature slugs continued to grow under cover throughout July because those collected in August were bigger than those in June. Mature slugs disappeared from the samples in July. The appearance of fresh, plump and glossy mature slugs in August indicated that they developed from immature slugs and that the emaciated mature specimens collected in June died during July.

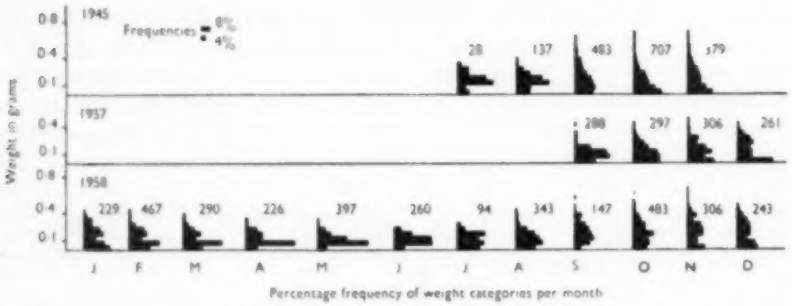

Fig. 2.—*Arion hortensis* : percentage frequency of weight categories per month in 1945, 1947 and 1958. The numerals denote the numbers of slugs from which the histograms are calculated.

These results suggest that *A. hortensis* does not live much more than a year, in this respect resembling other members of the genus (*A. subfuscus* and *A. ater*) that have been observed. More details of this annual cycle can be obtained only by experiments on the behaviour of this slug under known physical conditions at all stages of development.

ARION SUBFUSCUS

Barnes & Weil established that *A. subfuscus* was most numerous during June and July and that mating occurred only from July to October, and I have confirmed this.

The histograms (Fig. 3) of the prevalence of slugs in different weight categories, based on the percentage weights of the slugs collected per month for the years 1944, 1945 and 1958, show the growth of *Arion subfuscus* throughout the year. In October many young appear, grow slowly throughout the winter and rapidly in April. These reach maturity and disappear at the end of the summer as the new generation hatches. Unfortunately dissection of this species was confined to the period May to December (Fig. 4, a, b, c). Mature specimens occur only during the summer. Egg clusters were laid, by slugs awaiting dissection, in August and some of the earliest of these hatched in an unheated north-facing laboratory after about six weeks.

The growth period is the late autumn, winter, spring and early summer. Mating is restricted to the four months, July to October. I suggest that the rapid growth in May is associated with the spring flush of plant growth and

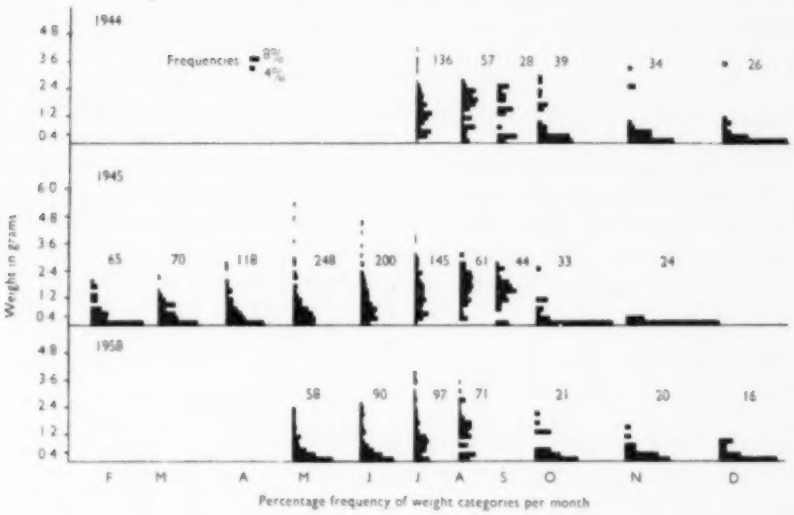
1944
Frequencies 8%
4%
136 57 28 39 34 26
1945
65 70 118 248 200 145 61 44 33 24
1958
58 90 97 71 21 20 16
Weight in grams
0·4 1·2 2·4 3·6 4·8 6·0
F M A M J J A S O N D
Percentage frequency of weight categories per month

Fig. 3.—*Arion subfuscus* : percentage frequency of weight categories per month in 1944, 1945 and 1958. The numerals denote the numbers of slugs from which the histograms are calculated.

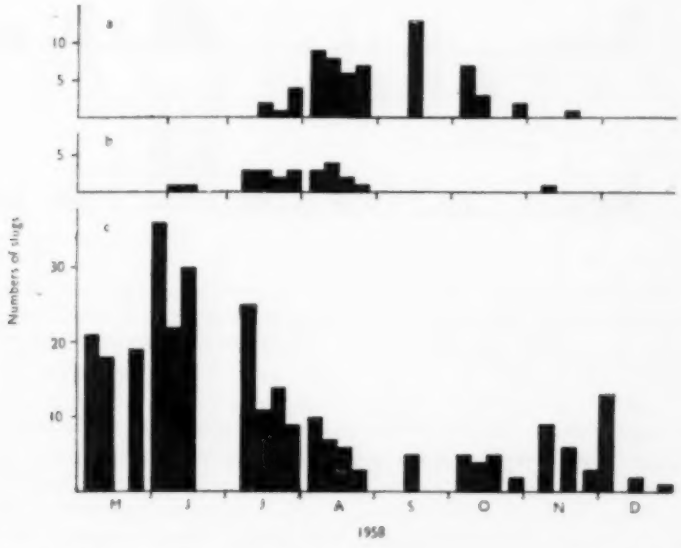

Fig. 4.—*Arion subfuscus* : numbers of (a) mature-mated, (b) mature-unmated and (c) immature slugs collected in 1958.

that the weather in the autumn affects the time at which egg-laying and hatching occur.

AGRIOLIMAX RETICULATUS

Barnes & Weil showed that this species is most active in July and August and least in January and February. They also observed that this species mates all the year, but most frequently between August and October. In the present study the same activity cycle is apparent. All categories of this slug occur throughout the year (Fig. 5, b, c, d) and there is scarcely a month without egg-laying. The weight histograms (Fig. 6) show a large increase of the smallest slugs in May 1945 and in June 1958, and in both years this

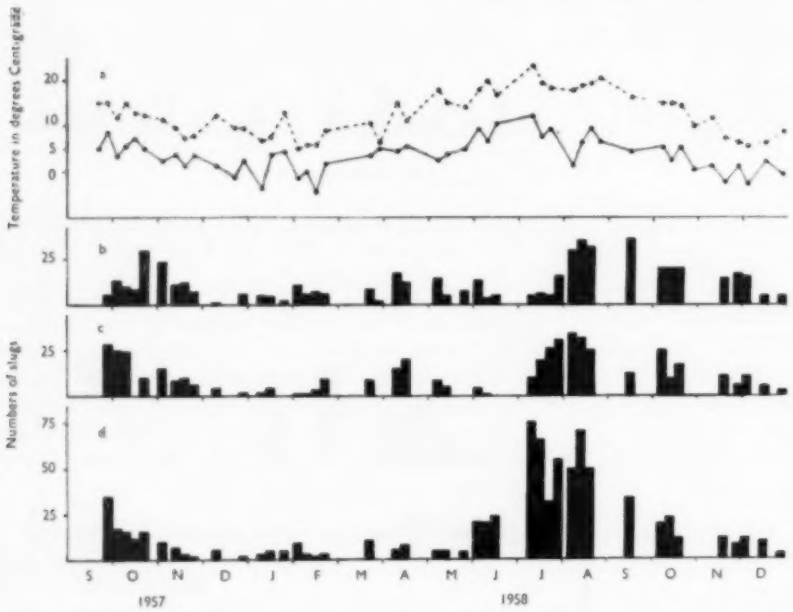

Fig. 5.—*Agriolimax reticulatus*: (a) the maximum air temperature (dotted line), minimum temperature on the grass measured at Rothamsted Meteorological Station and numbers of (b) mature-mated slugs, (c) mature-unmated slugs, (d) immature slugs collected in 1957 and 1958.

influx of young shows itself in the heavier weight categories during the months that follow. In 1945 the lightest weight category predominates again in October and November. No such increase in young appeared in 1944, 1957 or 1958, but it was observed that some slugs awaiting dissection during late July and August 1958 laid eggs in the tubes. These phenomena can be explained by the laboratory observations of Carrick (1938 & 1942), who found that the incubation period becomes longer and mortality greater as temperature

decreases, that the rate at which individual eggs in an egg-mass develop varies considerably, and that this heterogeneity increases as the temperature decreases. Coe (1944) stated that abundance of food encourages the production of eggs and Carrick (1938) stated that damp conditions encourage oviposition.

The influx of newly hatched slugs in May and June 1958 can be accounted for by the overwintering adults responding to the spring growth of vegetation. Their eggs hatched in about 2½ weeks because of the temperature prevailing (Fig. 5 a) at that time of year (Carrick, 1938). The slugs grew rapidly during the summer and became mature in late July and August.

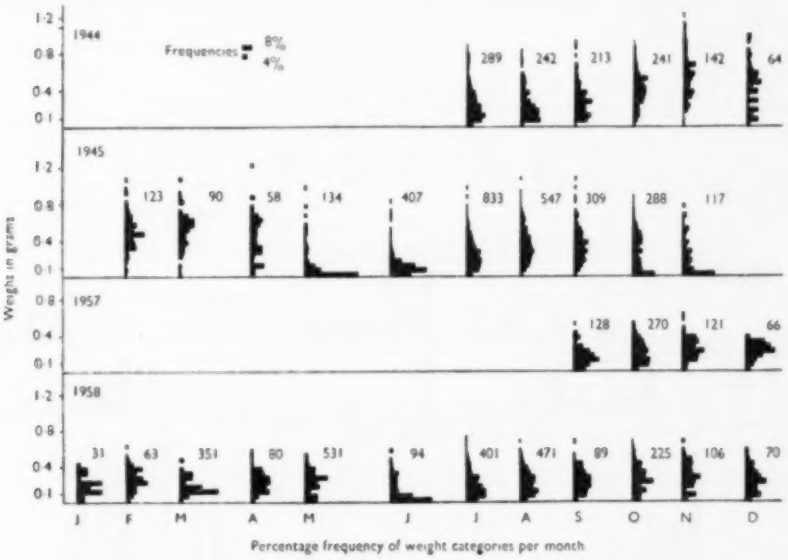

Fig. 6.—*Agriolimax reticulatus* : percentage frequency of weight categories per month in 1944, 1945, 1957 and 1958. The numerals denote the numbers of slugs from which the histograms are calculated.

The fate of eggs laid in the autumn depends on the weather. The colder the autumn the longer the incubation period and the greater the mortality. This means that there is less likelihood of an obvious influx of newly hatched slugs in the autumn. The slugs that hatch from these eggs develop more slowly than those in the summer, mate and lay eggs during the winter but it is not until the spring, when conditions for egg-laying and development are really favourable, that any rapid change in the age-grouping of the population is again apparent.

MILAX BUDAPESTENSIS

Collections of *Milax budapestensis* from 5 Moreton End Lane were much smaller than reported by Barnes & Weil, but nevertheless the same cycle of

activity is apparent. This slug is most active during September and October and, like *A. hortensis*, least active during June and July. Fig. 7 summarizes the results of the dissections.

Immature slugs are fewest from January to June and more numerous between August and November (Fig. 7). The number of mature-unmated slugs is at its greatest between September and December (Fig. 7 c). The mature-mated individuals are most numerous from January to the beginning of May (Fig. 7 d). The average weight of mature (mated and unmated) is greatest in September and October (Fig. 7 a) and decreases throughout the winter and spring. All the mature slugs of the previous year have disappeared by the end of July. The average weight of immature slugs is lowest in January and highest in July.

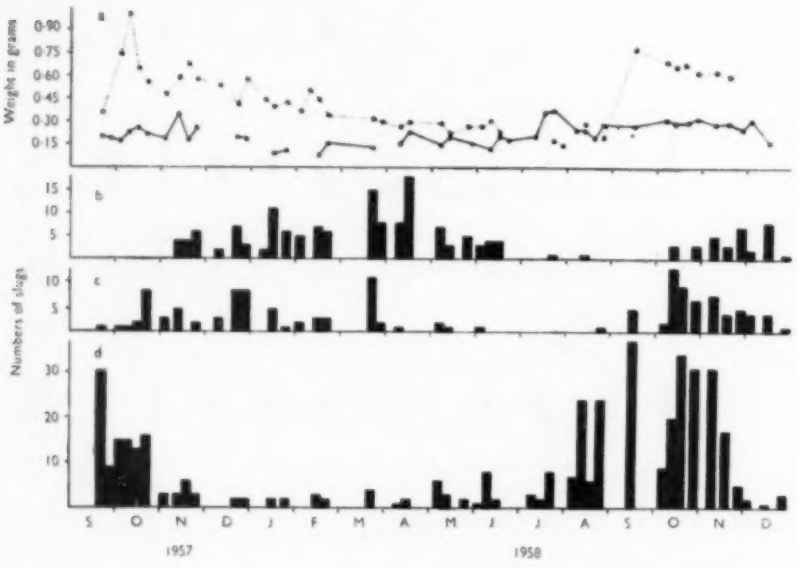

Fig. 7.—*Milax budapestensis* : (a) average weight of mature slugs (dotted line), immature slugs (full line) and numbers of (b) mature-mated, (c) mature-unmated, (d) immature slugs collected in 1957 and 1958.

M. budapestensis passes a very robust spermatophore at mating. A record was kept when they occurred in the dissections. Two spermatophores were sometimes found in the spermatheca, one more disintegrated than the other, showing that two matings had occurred. In the dissected slugs the whole spermatophores first appeared on 11th November, became more numerous and then decreased in numbers. From February until the middle of June only digested spermatophores were present. Later still only fluid remained in the spermatheca. The presence of whole spermatophores indicates that mating took place from November to February.

Although *M. budapestensis* was a co-dominant species when Barnes & Weil were collecting, it was a comparatively rare species in 1957 and 1958. Very small individuals featured in their collections, but few appeared in mine. Nevertheless it is possible to draw a generalized picture of its life cycle (Fig. 8). Mating takes place in the autumn and winter. In some years, e.g. 1944 and 1945, hatching occurs as early as October. Growth of this burrowing species may not be affected as much by weather changes as is the growth of

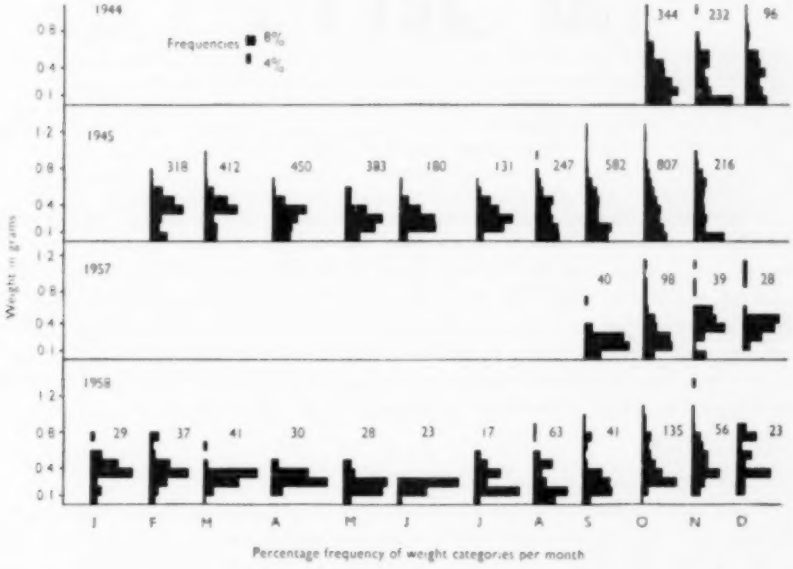

Fig. 8.—*Milax budapestensis*: percentage frequency of weight categories per month in 1944, 1945, 1957 and 1958. The numerals denote the numbers of slugs from which the histograms are calculated.

A. reticulatus which is a surface slug. Growth apparently continues throughout the winter, spring and summer culminating in maturity in the autumn. In 1958 the first mature slugs were collected in October and the first sign of mating was seen on 11th November.

MILAX SOWERBII

Few individuals of this species were collected as by Barnes & Weil, and I also confirmed their conclusion that it is most active in August and September and least in December and January.

Fig. 9 summarizes the results of the dissections and shows that mating starts towards the end of September. This species, like *M. budapestensis*, exchanges extremely tough spermatophores, which were first found in spermathecae during September. The spermatophores found in December

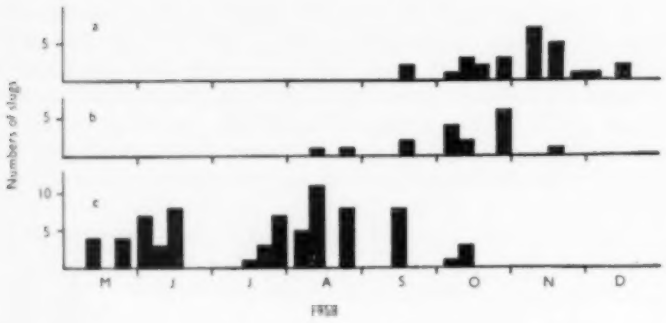

Fig. 9.—*Milax sowerbii* : numbers of (a) mature-mated, (b) mature-unmated and (c) immature slugs collected in 1958.

were beginning to disintegrate showing that the intensity of mating was then starting to wane. Unfortunately the dissections of this species were not started until May, but the young began to be collected in February. Newly hatched specimens were never collected. Only one mated individual was found between May and the end of August. I suggest that this species hatches in early spring, grows throughout the summer to become mature and mates in September, October and November. Egg-laying starts during these three months, after which the adults presumably soon die.

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SOME CONTROVERSIAL ASPECTS OF SPECIATION OF AFRICAN CICHLID FISHES

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A clear distinction must be made between the intralacustrine speciation shown by some groups of African cichlid fishes and the simple specific proliferation shown by others. The former phenomenon is exhibited by several genera but hardly at all by the genus *Tilapia*.

Inshore dwelling habits and an algal diet have not had restrictive effects on speciation. In fact it is among inshore species that speciation has been most active.

While, partially by exploiting their small size, genera which have given rise to the endemic species flocks of the great lakes have become highly specialized for the exploitation of specific niches, the species of *Tilapia* have usually remained large and unspecialized and therefore capable of existing in a variety of environments.

Further consideration of the effects of predation supports the idea that it has accelerated rather than retarded the process of speciation.

If certain conditions are fulfilled, closely related species can co-exist throughout life in one habitat, eat the same kind of food and breed in close proximity to each other.

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INTRODUCTION

The existence of remarkable assemblages of cichlid fishes in African lakes has encouraged a number of zoologists to speculate on various aspects of their evolution. Although more and more concrete information on the biology of these fishes is now coming to hand full agreement has not yet been reached on several points. Thus a recent paper by Lowe (McConnell) (1959), which gives a valuable summary of certain aspects of the biology of members of the genus *Tilapia* also makes a number of suggestions with which other students will be unable to agree. Some of these points are discussed in the following paper which, it should be clearly understood, does not purport to level criticism at Lowe's factual data but only at certain of her conclusions.

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INTRALACUSTRINE SPECIATION AND SIMPLE SPECIFIC PROLIFERATION

It is perhaps unfortunate from the point of view of the student of evolution in African lakes that so much attention should have been directed to the genus *Tilapia*, for conclusions drawn from the study of this genus can be misleading if applied to other African cichlid fishes. The evolutionary history of the genus *Tilapia* is in fact quite different from that of *Haplochromis* and the other genera which constitute the species flocks of the great lakes. Thus although several lakes are inhabited by endemic species of *Tilapia* in only one, Nyasa, is there any suggestion of that intralacustrine speciation for which several other cichlid genera are so renowned. The occurrence of endemic species with little or no intralacustrine speciation—the almost inevitable result of geographical isolation—is not particularly remarkable and is in fact to be seen in several other genera of African fishes. In Lake Nyasa, where some intralacustrine speciation has taken place in the genus *Tilapia*, the resulting species flock comprises only four species, a fifth endemic species, *T. shirana* Boulenger, being obviously of different ancestry. This state of affairs compares strikingly with the situation in *Haplochromis* which has given rise to about seventy species in Lake Victoria and more than a hundred in Lake Nyasa, and with genera such as *Lethrinops* with twenty-four Nyasan species and *Lamprologus* with thirty-four species in Tanganyika. The speciation to which Lowe refers when she speaks of the extensive speciation of the maternal brooding species of the genus *Tilapia* is surely nothing more than the normal proliferation of species which one expects in a successful and widely distributed genus and is a quite different phenomenon from that which has attracted so much attention to African lakes. Specific proliferation of the type shown by *Tilapia* is for example exhibited in an equally or more striking manner by several genera of African fishes, such as *Gnathonemus*, *Marcusenius* and other mormyrid genera, by *Alestes* and *Distichodus* among the characins, by the silurid genus *Clarias*, and by cyprinid genera such as *Labeo*, *Barilius*, and particularly *Barbus*, none of which incidentally, are mouth brooders. Failure to differentiate clearly between these two types of speciation phenomena makes it difficult to understand the significance of statements to the effect that some groups of *Tilapia* have undergone " extensive speciation " (p. 9) and that others " have not speciated " (p. 11).

DIET, HABITAT AND SPECIATION

Lowe repeatedly mentions the advantages of open-water habitats to which she thinks that mouth-brooding species are pre-adapted, and suggests that both inshore-dwelling habits and an algal diet have acted as brakes to speciation (pp. 11, 12, 16, 17, 20, 26). So far as the genus *Tilapia* is concerned she to a large extent equates the frequenting of inshore habitats with the habit of substratum spawning (though later, p. 11, she extends this argument to inshore-dwelling mouth-brooders) and believes that because this group is confined by feeding and breeding habits to shallow waters its opportunities for speciation have been restricted. That mouth-brooding has advantages in African lakes and has been important in permitting intralacustrine speciation is not denied, but the reasons for my adherence to this view are not those

advanced by Lowe and are recorded elsewhere (Fryer 1959 b). It is quite true, as Lowe points out, that the inshore-dwelling species of *Tilapia*, both substratum spawners and mouth brooders, have not undergone intra-lacustrine speciation in African lakes, but this does not mean that the inshore habit is itself a brake on speciation. On the contrary it is just those species of cichlid fishes of other genera which live in the littoral zones of the great lakes that have undergone intralacustrine speciation to the greatest extent. No one denies the advantages of an open-water habitat—advantages which have been exploited by cichlids other than species of *Tilapia*, e.g. the *Haplochromis* species of the "Utaka" group in Lake Nyasa—but to claim that inshore conditions are less favourable to speciation than are those prevailing in open water is to ignore an overwhelming mass of evidence to the contrary.

The fact that a species is restricted to inshore waters does not necessarily mean, as Lowe seems to imply, that it is not a successful species nor, incidentally, as she infers in the case of *T. tanganicae* (Günther) in Lake Tanganyika, that it is kept there by predators, of which more anon. It is axiomatic that a species is in most respects well adapted to the habitat in which it occurs, and the fact that some species of *Tilapia* are undoubtedly successful as frequenters of open-water should not be allowed to obscure the fact that other habitats offer alternative advantages, or that the species of *Tilapia* concerned, ecologically euryvalent though they may be, may not possess all the requisite adaptations necessary to permit them to exploit open-water conditions. (See also p. 572.)

The idea that a vegetarian, and more specifically an algal, diet has had restrictive effects on speciation in the genus *Tilapia* is suggested by Lowe. My own studies on a group of endemic rock-frequenting cichlid fishes of Lake Nyasa have shown that such a diet is no disadvantage for no fewer than eleven closely related and co-existing species subsist largely or entirely on algae growing on rock surfaces, as do two other cichlid fishes of the genus *Haplochromis* which occupy the same general habitat (Fryer 1959 a). Neither the inshore habit nor an algal diet has prevented the development of this species flock which is in fact one of the most striking of all known examples of intralacustrine speciation. Data given by Poll (1956) on the gut contents of members of a group of Tanganyikan cichlid fishes with similar habits but with an independent evolutionary history suggest that here too an algal diet has by no means restricted speciation.

Most fishes tend to be carnivorous and the assumption of an algal diet may in fact have been an important evolutionary step in the history of these cichlid fishes and one which opened up a new series of niches for colonization. This seems to be the case in the rock-frequenting species mentioned above (and in the wider sense of the term speciation, in the genus *Tilapia* itself) and in the case of another group of freshwater organisms which shows several interesting parallels to these fishes, namely the cyclopoid copepods whose basic feeding mechanism is obviously that of a carnivore (Fryer 1957 a) but of which many species are now algal feeders (Fryer 1957 b). Although they seem to be in some ways not fully adapted to a vegetarian diet it is those genera which comprise the algal eating species which now contain the largest number of species.

THE ALTERNATIVE ROUTES TO EVOLUTIONARY SUCCESS

Although the suggested reasons for the lack of intralacustrine speciation in the genus *Tilapia* adduced by Lowe have been rejected it seems possible to point to an explanation of this phenomenon. The answer would appear to lie in the unspecialized nature of the genus. All species of *Tilapia* are very much alike, and trophic specializations—so important in the adaptive radiation of African cichlid fishes—seem to be confined to two types, weed chopping and fine particle feeding. The latter habit can enable its possessors to feed on either bottom material or on phytoplankton and some species at least are facultative feeders utilising whichever of these two sources of food is most readily available. The unspecialized nature of several species is revealed by their wide geographical distribution within which they frequent habitats of considerable diversity ; the great tolerance of several species in the latter respect being in large measure a reflexion of feeding habits, for few habitats lack organic bottom detritus. Lowe refers to the wide distribution of some of the substratum spawners, but certain mouth-brooding species such as *T. galilaea* (Artédi), *T. nilotica* (L.) and *T. mossambica* (Peters) are also wide ranging species. *T. galilaea* has a range extending from Senegal and the Gambia, through the Niger and Volta, and much of the Nile system to the Jordan Valley, while *T. nilotica* covers much the same area but also extends further south into the Congo system. Within this vast range both species frequent both riverine and lacustrine habitats. The adaptability of many species of *Tilapia* to fish-pond conditions and the way in which introduced species often establish themselves in new environments also reveals the unspecialized nature of members of this genus. The importance of specialization in speciation in African lakes has been pointed out elsewhere (Fryer 1959 b) and it is an incontravertible fact that the vast majority of the endemic cichlids of the great lakes are highly specialized for life in one particular environment. One could not, for example, conceive of any of the rock-frequenting species of Lakes Nyasa and Tanganyika existing under the range of ecological conditions tolerated by *T. nilotica*.

Another difference between the genus *Tilapia* and those genera which have undergone much intralacustrine speciation, and one which to a large extent reflects the unspecialized nature of the former and the specializations of the latter, is size. Almost without exception members of the genus *Tilapia* are larger than are members of the species flocks of other cichlid genera. Now, Hutchinson (1959) has recently demonstrated that small size, by permitting animals to become specialized to the conditions offered by small diversified elements of the environmental mosaic, permits a degree of diversity quite unknown among groups of larger organisms. (See also Hutchinson & MacArthur 1959). Few groups can provide a more elegant demonstration of this principle than these cichlid fishes.

The larger size of the species of Tilapia which have colonized the lakes must also to a large extent render them immune from the effects of predation which I believe to have been a stimulus and not a brake to speciation in their smaller brethren (see below). Some predation can of course be expected during the

early stages of development, but, if Garrod's (1959) findings concerning the growth of *Tilapia esculenta* Graham are at all typical of the genus as a whole—and the indications are that some species grow more quickly than this one—then after one year's growth, by which time they have achieved a length of some 15 cm., individuals of this species are already larger than the adults of many other lacustrine cichlids, and after two years, when they have grown to a length of about 19 to 21 cm., they are too large to be eaten by many predators.

During the evolutionary history of the African cichlids therefore it would appear that, in general, the lacustrine forms have specialized for life in certain environments while the genus *Tilapia* has adopted the alternative evolutionary possibility and has remained unspecialized. While the taking of the latter course has necessitated forfeiture of the opportunity of undergoing great adaptive radiation in the lakes it has paid dividends in other ways and has given rise to several adaptable, highly successful, and wide-ranging species.

THE EFFECTS OF PREDATORS—A SUMMARY OF RECENT EVIDENCE

Lowe also enters the controversy regarding the effect of predators and takes her stand alongside Worthington who believes that the existence of predators, particularly *Lates* and *Hydrocyon*, has had a restrictive effect on intralacustrine speciation. Several papers relevant to this controversy were in the press at the same time as that of Lowe and all contain either factual or theoretical evidence, or both, which is opposed to this view.

A mortal blow has been dealt to this theory by the discovery of fossils of *Lates* in Holocene deposits from Lake Edward (Greenwood 1959 b). This means that, contrary to Worthington's view, *Lates* and the speciating *Haplochromis* flock of Lake Edward co-existed until very recent times. Even after taking into account extenuating circumstances, to which Greenwood gives full consideration, such as the fact that the Lake Edward cichlids were apparently derived from partially specialized ancestors from Lake Victoria, the blow to Worthington's hypothesis is a telling one.

Other facts, derived from work in Lake Nyasa, which suggest that predators have hastened rather than retarded speciation, have been given in some detail elsewhere (Fryer 1959 a, 1959 b), and a very similar conclusion, at least in so far as concerns the part played by predacious species in keeping the population density of the prey species at a level low enough to prevent much interspecific competition and, by inference, preventing the elimination of species, has been reached independently by Greenwood (1959 a) as a result of his studies on the *Haplochromis* flock of Lake Victoria. Details of these studies need not be repeated here, but the evidence adduced by Lowe in favour of Worthington's theory must be dealt with.

First she repeats Worthington's idea that " incompletely adjusted forms " will be selected against when predation pressure is high, and that abnormal forms occur more often in the *Lates* and *Hydrocyon*–free lakes, Victoria and Edward, than in Lakes Albert and Rudolf in which these predators occur. As pointed out elsewhere (Fryer 1959 b) the elimination of the unfit is an accepted process of evolution and will favour speciation and not retard it. The removal of malformed individuals, of whose incidence more precise data

are required before they can be regarded as significant, would have this beneficial effect on speciation.

Lowe then refers to the fact pointed out by Fryer & Iles (1955) that Lake Nyasa, although lacking *Lates* and *Hydrocyon*, has many predators, both cichlid and non-cichlid. She rightly points out that the predatory cichlids of the lake tend to be small and that *Bagrus* and the clariids (some, formerly placed in the genus *Clarias*, now being referred to the endemic genus *Bathyclarias* (Jackson 1959)), which are among the most important non-cichlid predators of the lake, appear to be " lurking " rather than " swift " predators. It may appear intuitively obvious that such predators are of less significance than the very obviously piscivorous *Lates* and *Hydrocyon*, but consideration of concrete data reveals that the above facts in no way minimise the importance of these fishes as predators. Thus the species of *Rhamphochromis*, while relatively small, are quite large enough to prey heavily on other cichlids, many species of which never achieve a total length of 20 cm. In the case of *Bagrus* and the clariids the way in which the food is obtained is quite irrelevant* ; the important thing is that members of these, and other genera, do undoubtedly prey heavily on cichlid fishes. Thus a very large body of data concerning the food of some three thousand specimens of *Bagrus meridionalis* Günther, which conclusively demonstrates its predatory nature, has recently been collected and prepared for publication by Mr T. D. Iles.

The same is true in Lake Victoria where species of *Bagrus* and *Clarias* are similarly important predators and from which lake precise data relating to the food of large numbers of these fishes are now available. Thus in this lake Corbet (1959) has shown that of a sample of more than a thousand specimens of *Bagrus docmac* Forskål more than 78 per cent had fed on cichlid fishes, and that even this total was probably lower than the true figure because a small proportion of fish remains could not be identified with certainty. Similarly over 80 per cent of almost four hundred specimens of *Clarias mossambicus* Peters were shown to have fed on cichlid fishes. That both these species, and particularly *B. docmac*, are abundant in the lake is readily shown by examination of figures for fish landings in 1957 recorded by the Lake Victoria Fisheries Service (1958). These figures show that about half a million *Bagrus* and a smaller number of *Clarias* passed through the recording stations (which by no means record all landings), and that members of these two genera comprised some 12 per cent of the total recorded commercial catch made in gill nets of 4 inch mesh and above in both the Kenya and Uganda waters of the lake, and that in Tanganyika waters their contribution to the total catch in this range of nets was as high as 85 per cent! Approximate though these figures are and biased as the figures for Tanganyika waters may be by the locations of the sampling stations, it is obvious that to argue that

*One way in which these " lurking " predators may find it possible to capture active prey is by being active at times when the prey is " sleeping ". This happened in an ornamental aquarium into which I introduced juvenile specimens of *Tilapia variabilis* Boulenger and a young *Clarias mossambicus* Peters. By day all was well but at night, when the young *Tilapia* rested, havoc was caused by the *Clarias*. A similar fate befell specimens of *Lebistes* which definitely " sleep " at night, though by day their nimbleness was such as to enable them to evade the young *Clarias*.

predation of this order of magnitude is less important than that exercised by fishes which to the popular imagination are better suited to the role of predator is to ignore a mass of concrete data.

Of interest too in the present connexion is the fact that Corbet's figures show that *Bagrus* and *Clarias* prey far more heavily on *Haplochromis* than on *Tilapia* in Lake Victoria yet it is the former and not the latter genus which here exhibits intralacustrine speciation. These data lend support to the idea expressed elsewhere that predation favours and does not retard intralacustrine speciation.

Lowe also refers to the fact that in Lakes Albert and Rudolf, in both of which are found *Lates* and *Hydrocyon*, the species of *Tilapia* present (none of them endemic) frequent inshore waters (as does *T. tanganicae* in Lake Tanganyika mentioned above) whereas in lakes lacking these predators they have open-water living phases. Apart from the fact that this is not true for *T. nilotica* in Lake Edward this explanation cannot be accepted without question. In Lake Edward, which contains neither *Lates* nor *Hydrocyon*, Lowe herself (Lowe (McConell) 1958), quoting Worthington who presents data which flatly contradict his theory, states categorically that " the typical habitat [of *T. nilotica*] is the comparatively shallow inshore water " and that " this species does not occur in the deep water of Lake Edward except occasionally at the surface ". A partial explanation of a different kind has been mentioned above (p. 571) but it might be noted further that general ecological conditions reflecting the morphometric characteristics of the lake should not be overlooked as factors influencing intralacustrine distribution. In the southern part of Lake Nyasa *Tilapia* of the *saka-squamipinnis* group frequent open waters and feed by preference on phytoplankton (Lowe 1952) but in the north, where more precipitous shores prevail, they are found inshore and feed on material accumulating on the bottom (Fryer 1959 a). These differences in ecological distribution obviously reflect lake morphology and have nothing to do with the presence or absence of *Lates* and *Hydrocyon*. There is indeed a world of difference between, for example, Lakes George and Albert, and it would be a very credulous ecologist who would expect that a given species would have the same sort of distribution in each of these basins.

Relevant to this too are some of Lowe's own observations on *T. nilotica*. This fish has been introduced into several small predator-free lakes to which it is not indigenous and in these its distribution, to use Lowe's own words, " depends on the ecological conditions ". In some lakes it is evenly distributed, as in Lake George ; in others it occurs in localised areas where there are stands of aquatic plants (Lowe (McConnell) 1958).

Furthermore, one would expect on *a priori* grounds that phytoplankton feeding fishes would exhibit a preference for inshore rather than offshore waters in African lakes, for it is in inshore waters of all save the smallest and shallowest lakes that the greatest concentrations of phytoplankton are to be found (Ross 1955). It is also important for those unacquainted with African lakes to realise that, no doubt in part as a consequence of the above fact, some of the so-called open-water species are certainly not pelagic in the way in which are fishes of the open seas but are in fact confined essentially to inshore waters.

This applies, for example, to *T. esculenta* Graham and *T. variabilis* Boulenger in Lake Victoria—a lake lacking *Lates* and *Hydrocyon*. Work from the time of Graham's survey some thirty years ago to the present has shown that, save in closed gulfs and sheltered regions where offshore islands occur, *T. esculenta* is seldom found more than five miles off shore and even in the most sheltered regions is seldom or never found more than twenty miles from land. Similarly *T. variabilis*, while exhibiting rather different ecological preferences, is also concentrated in a relatively narrow belt of inshore water.

It must also be pointed out that those who would argue that predators serve to restrict other species to inshore waters are thereby surely damaging their own case for the restrictive effects of predators on speciation, for it is species which are so ecologically restricted which, in spite of what may have been said to the contrary, have undergone the most abundant speciation in the great lakes.

As a further point held to be evidence of the importance in this connexion of *Lates* and *Hydrocyon* Lowe refers to the fact that in Lakes Albert and Rudolf " the fish of many genera are much larger than their counterparts in the other lakes and the *Tilapia* tend to have longer stronger spines ". Of the reasons which *could* conceivably be responsible for this the effect of predators is only one and the suggestion would appear to be quite incapable of proof. The fact that Lowe refers to genera and not to species also betrays a further weakness in the argument. Thus *T. melanopleura* Duméril is much larger than *T. sparrmani* A. Smith but one cannot say why save that the difference is genetical. Even if identical species were involved or implied the argument would be false. This is adequately demonstrated by the widely divergent growth patterns of any of several species of fishes when grown in different types of fish ponds.

As to stout spines, the strongest I have seen in any species of *Tilapia* are those of a species now being studied which inhabits Lake Kitangiri in Tanganyika Territory. If, as I believe, this has nothing to do with predation, then the suggestion made concerning the stout-spined specimens from Lakes Albert and Rudolf loses much of its weight. If, on the other hand, there is a connexion between stout spines and predation, then other predators must exert similar effects, because of predacious species only *Clarias* and *Protopterus* (a " mild " predator) occur in Lake Kitangiri.

REPRODUCTION AND ECOLOGICAL ISOLATION IN RELATED SPECIES

An interesting fact discovered by Lowe is that, in Lake Nyasa, while three very closely related species of *Tilapia* feed together on the same food they breed in different situations and at different times of the year. However, it is misleading to think that this type of behaviour, which to a large extent parallels that of certain birds, is essential in order to permit closely related and frequently meeting species to remain distinct as Lowe suggests. On the contrary it is possible for species to live together and to breed in close proximity to each other at all times of the year and yet remain distinct ; and it is surely in such cases, of which the rock-frequenting Nyasan cichlids are an outstanding

example, that differences in breeding behaviour patterns, to our knowledge of which Lowe has herself made significant contributions, become supremely important. Instead of saying, as does Lowe, that " ecological isolation need not, however, be complete throughout life " one is tempted to go so far as to say that ecological isolation need not exist provided that food is superabundant (as seems often to be the case among feeders on both lithophilic and planktonic algae), that the population density is controlled by predators or some other means, and that different species have different patterns of breeding behaviour (particularly courtship, as may be deduced from the striking and specific colour patterns of the males) which assist in the maintenance of interspecific sterility barriers. Here again the small size of some of the cichlids exhibiting these phenomena may have been important in permitting them to split up for breeding purposes one major habitat and to do so to such an extent that it has so far proved virtually impossible to discern differences in the territories selected by the males of closely related and co-existing species.

SUMMARY

Some controversial topics relating to the evolution of cichlid fishes in African lakes are discussed and certain recently published suggestions are refuted. It is shown that a clear distinction must be made between the phenomenon of intralacustrine speciation as shown by several cichlid genera and that of mere specific proliferation as shown, save to some extent in Lake Nyasa, by the genus *Tilapia*. Failure to differentiate clearly between these phenomena has led to considerable confusion in the past.

The recently expressed idea that inshore dwelling habits and an algal diet have had restrictive effects on speciation is shown to be unfounded. It is in fact among the inshore dwelling species that the greatest amount of speciation has taken place in African lakes.

Different evolutionary routes, each of which has led to success, have been taken by those genera which have given rise to the endemic species flocks of the great lakes, and by the genus *Tilapia*. The former, partially by exploiting their small size, have become highly specialized for life in one of several possible environments and usually for the collection of one type of food. By contrast the species of *Tilapia* have, with few exceptions, remained large and unspecialized, and this has enabled individual species to exist over wide geographical areas in a variety of environments.

Recent views on the effects of predation on evolution in the great lakes are considered and concrete data having a bearing on this question are reviewed. This evidence very strongly suggests that the old idea that predators (of which fishes other than *Lates* and *Hydrocyon* are shown to be important) have had a restrictive effect on speciation, is unfounded. In fact a good case can be made out for the reverse role—that of accelerating speciation—for these fishes.

It is emphasized that closely related species can co-exist throughout life in one habitat, where they may even take the same food and breed in very close proximity to each other, provided certain conditions are fulfilled. The importance under such circumstances of that part of the reproductive behaviour leading up to the shedding of gametes is emphasized.

ACKNOWLEDGMENT

I should like to thank Mr Hugh Y. Elder for discussing this paper with me and for drawing my attention to a point which had escaped my notice.

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DENTITION OF THE RIBBON SEAL

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(With 3 plates)

The dental formula of *Histriophoca fasciata* is : I 3/2, C 1/1, PC 5 (rarely 6) = 34 to 36. The teeth are rather weak, smooth and distantly spaced. The lower incisors are only half the size of the upper ones and are frequently lost. The lower canines point outward at an angle of 45° from the horizontal. In each half of the jaw, upper and lower No. 1 is the smallest of the postcanine series ; Nos. 3 and 4 are the largest ; Nos. 2 and 5 are nearly equal. On some skulls the gap between upper postcanines Nos. 4 and 5 is distinctly the widest. The upper postcanines may have a small posterior cusp ; the lower ones frequently have both anterior and posterior cusps. In each half of the jaw, upper and lower postcanine No. 1 is single rooted ; No. 5 is double rooted ; Nos. 2, 3 and 4 are transitional.

On one specimen, the third pair of upper postcanines is missing and all of the teeth are unusually small. This skull may be pathological or it may be evidence of the variation to be expected in a declining evolutionary form.

Male and female are similar in body size and may reach a length of at least 170 cm. and a weight of at least 95 kg. Cranial measurements of five adult males, one adult female and one adult sex-unknown are given.

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INTRODUCTION

The genus *Histriophoca* Gill 1873 contains a single species, *H. fasciata* (Zimmermann) 1783, the ribbon seal. This seal lives among the drift-ice floes of Okhotsk, Bering and Chukchi seas (Scheffer, 1958, map on p. 104). It does not come on land. Its nearest relative is the harp seal, *Pagophilus groenlandicus* (Erxleben) 1777, of the North Atlantic Ocean and adjacent seas.

The genus *Histriophoca* was the last of twenty genera of pinnipeds to be distinguished. Even today, few skulls of the ribbon seal are in museum collections. As recently as 1942, Doutt (p. 93) could find only two adult specimens for study ; as recently as 1951, Mohr (p. 192–3) was first to publish photographs of the skull. It was therefore a pleasure to receive in 1959 from Dr Francis H. Fay a well-prepared adult skin and skull. Because of certain odd features of dentition, the Fay skull is referred to as " anomalous BDM

548 ", though at the moment it is not certainly known how anomalous it is. Later it will be compared with one subadult and four adult skulls.

The first purpose of this paper is to describe the dentition of the ribbon seal in the light of new information ; second, to discuss the zoological significance of anomalous BDM 548 ; third, to summarize what is known about size of skull and body in adult ribbon seals. Size data are a clue to age, or at least relative age, of the individual.

DENTITION

(*a*) *General*

The dental formula (Pl. 1) is the same as in all members of the subfamily Phocinae (northern phocids) : incisors $\frac{1\text{-}2\text{-}3}{0\text{-}2\text{-}3}$, canines $\frac{1}{1}$, postcanines (premolars and molars) $\frac{1\text{-}2\text{-}3\text{-}4\text{-}5\text{-}(6)}{1\text{-}2\text{-}3\text{-}4\text{-}5\text{-}0} = 34$ to 36. A sixth upper postcanine has been reported once (Von Schrenk, 1859, *fide* Mohr, 1951, p. 191). In general the teeth are fairly weak, smooth and conical ; spaced well apart ; the front ones directed forward and outward, with recurved tips. When jaws are closed and teeth are interlocked, each lower canine and postcanine is situated just forward of its upper counterpart. On the evidence of six skulls, the teeth are variable in size and in number of roots. As in all northern phocids, however, the incisors, canines and first postcanines are single rooted. Sexual dimorphism in teeth of *Histriophoca* has not been reported. The present specimens include skulls of five males and one sex-unknown.

(*b*) *Upper incisors*

The upper incisors on each side of the rostrum increase in size from No. 1 (medial) to No. 3 (lateral). No. 3 is caniniform and is twice as large as either No. 1 or No. 2. No. 3 may reach a height above the jawbone of 8 mm. All upper incisors are flattened laterally (right-and-left) and are set squarely across the tip of the rostrum. In anomalous BDM 548 the upper incisors are typical in shape though reduced in size ; No. 3 is 5 mm. high.

(*c*) *Lower incisors*

The lower incisors are fragile and variable in size. According to Naumov and Smirnov (1936, p. 172) they often " fall out before their time ". A complete set is present in three of our six specimens. The lower incisors are only one-half the size of the uppers ; a generic character. The lateral one of each pair is slightly larger than the medial. (In USNM 311771 the lateral incisor is quite robust, twice as large as the medial. In this specimen, however, the tips of the mandibles have been repaired with opaque cement, and the teeth now in the sockets of lower incisors No. 3 are quite certainly the first upper postcanines of this or some other skull.) The direction of the tooth-size decrease, i.e., from the lateral to the medial incisor, and the evidence of a distinct gap in the tooth row above the mandibular suture tend to support the common belief that the lower incisors of modern phocids represent primitive Nos. 2 and 3, while primitive pair No. 1 has disappeared from the medial position. We shall, therefore, refer to the modern lower incisors on each side as Nos. 2

and 3. The lower incisors are arranged in the jaw like their opposites above. No. 3 reaches a height of 4 mm. in two skulls. In anomalous BDM 548 the lower incisors are denticles about 1 mm. in diameter, barely clearing the surface of the jawbone. They would have been hidden in the gum of the fresh specimen.

(*d*) *Canines*

The canines are not remarkable ; they resemble those of many phocids. In both upper and lower jaws they attain a height above the bone of 10 mm. and an anteroposterior diameter of 7 mm. The lower canines are directed forward and outward. As seen from the front they make an angle of 45° with the horizontal. The upper canines are also directed forward, though not always outward. In anomalous BDM 548 they are typical in shape though reduced in size.

(*e*) *Upper postcanines*

These are nearly alike in size. No. 1 is always the smallest. Nos. 3 and 4 are slightly larger than Nos. 2 and 5. The gaps between postcanines are distinct, approaching 1-tooth width. Gap No. 4–5 tends to be widest, and may be twice as wide as any other gap.

The crown of each upper postcanine rises to a sharp, slightly recurved, central point. Each of the five teeth tends to have an insignificant cusp on the posterior side. This cusp is barely visible on the teeth of subadult skull CMVZ 51385 and is worn completely from the teeth of old individual CMVZ 51387. The roots of the upper postcanines vary widely. No. 1 is clearly single rooted, though it may show a faint longitudinal furrow on the lingual side. No. 5 is double rooted, with a shallow-to-deep, forked indentation at the tip. Nos. 2 to 4 are transitional and variable. In PSM 7889 they may be called single rooted, with a faint furrow down the lingual side and a still fainter furrow down the buccal side. In CMVZ 51387, they are double rooted. In anomalous BDM 548, upper postcanines No. 3 are absent, apparently from birth. All other postcanines of this skull are small and weak. No. 1 has a cross-section diameter at neck of only 2·2 × 2·6 mm.

(*f*) *Lower postcanines*

The rank by size of the lower postcanines resembles that of the uppers, though lower No. 1 is always *much* the smallest of the series. Its evolutionary development has been suppressed by the deeply set, encroaching root of the nearby canine. Spacing of the lower postcanines resembles that of the uppers, though lower postcanine No. 5 has not been free to migrate backward and hence gap No. 4–5 is not especially wide. In contrast to the upper ones, each lower postcanine tends to have a small cusp on the anterior, as well as on the posterior, face. The anterior cusp is not always present. The root pattern is like that above, i.e., No. 1 single, Nos. 2 to 4 transitional and variable, and No. 5 double. In anomalous BDM 548, lower left postcanine No. 1 is a denticle only 1·9 mm. in diameter, worn to the gum-line.

ANOMALOUS SKULL BDM 548

From the appearance of a longitudinal section of the right upper canine (cut and polished by Clifford H. Fiscus) specimen BDM 548 represents a fully adult animal, though of uncertain age. On the pelt, the claws are faintly marked by transverse ridges, low in relief, each ridge paler than the valley on either side. Although ridges can be counted on each of the twenty claws, they are most clearly seen on the first digit of the fore flipper. Here the claw, 51 mm. in length, has 11 ridges (or perhaps 13, depending on the observer's judgment as to boundaries of the proximal and distal ridges). The ridges may represent annual periods of growth.

As previously stated, all the teeth of BDM 548 are small, and one pair is missing. So few specimens of this species have been examined by zoologists that it is impossible to judge how widely deviant the dentition of this skull may be. Chapskiy (1955, p. 196) discussed certain cranial features of the ribbon seal " which are typical of oppressed [vanishing] forms ", though he wisely concluded that " our knowledge of the ecology of the ribbon seal is . . . still insufficient for the clarification of this problem ". Partly because of the wide individual variation displayed in number and location of teeth, the beaked whales (Ziphiidae) are regarded by many zoologists as a declining evolutionary group. *Histriophoca* might be so regarded as well.

Chapskiy interpreted the simplified dentition and certain other skull features of the ribbon seal as adaptations for catching agile, soft-bodied prey at great depths. " Judging from the data of G. A. Pikharev (1939) and especially of V. A. Arseniev (1941), the ribbon seal feeds predominantly on deep-water fishes (mainly *Theragra chalcogramma* [pollack]) and on cephalopod molluscs, during spring near Sakhalin Island." Wilke (1954, p. 223) found, in ribbon seals killed in April near Hokkaido, pollack in two stomachs and squid in one of these stomachs. Rass *et al.* (1955) have stated in general terms that the ribbon seal feeds almost entirely on fish ; also molluscs ; seldom crustaceans. Crustaceans are perhaps the main food of the young seal. Adults are pelagic feeders in upper waters but also in depths of 100 metres or more. Other authors (Bobrinskoi, 1944 ; Naumov, 1933, 1941 ; Inukai, 1942) have supposed that the diet includes fish, cephalopods, and crustaceans.

The zoological significance of anomalous BDM 548 is not clear. It is either a pathological or undernourished skull—though its cranial features aside from teeth seem to be normal–or a marginal example of the wide variation to be looked for in a vestigial form. Further study of variation in the dental pattern of *Histriophoca* is needed.

SKULL AND BODY SIZE

Cranial measurements of seven adult ribbon seals are listed in Table 1. Two sets of measurements are from the literature. On the five adult skulls we have examined, the basioccipital-basisphenoid suture, one of the last to knit, is at least half closed. On one skull (CMVZ 51387) it is completely closed ; the bones are smooth and dense ; the teeth are worn.

Mohr (1951, p. 188) published a photograph of a male skull said to have a CBL of 198 mm. Some years ago we measured a skull, sex unknown, USNM

TABLE 1

Cranial measurements (millimetres) of adult ribbon seals[1]

	Specimen No. and Sex						
	CMVZ 51387[2] M	BDM 543[3] M	NAUMOV 1930–9[4] M	PSM 7889[5] M	BDM 548[6] M	NAUMOV 1930–8[7] F	USNM 311771[8] ?
Condylobasal length	201	201	199	194	193	193	193
Basilar length of Hensel	179	179	—	171	172	—	—
Mastoid width	133	127	128	116	130	127	122
Zygomatic width	128	—	124	124	127	125	—
Height at otic bullae	89	81	90	81	85	83	80
Palatal length	78	73	76	71	70	74	65
Interorbital width	16	16	15	12	14	12	14
Length of nasals	39	37	31	35	41	32	42
Width of nasals	18	—	18	19	16	15	16
Alveolar length of upper molar series	44	46	42	41	37	42	44
Alveolar length of lower molar series	41	41	37	39	35	36	40
Width of narial opening	27	29	29	29	26	27	28

[1] For definition of measurements, see Grinnell *et al.* (1937). Note that the " interorbital width " of those authors and the present writer is the distance between two parallels dropped from above the skull. Most of our measurements are shown diagrammatically by Hall (1946, p. 679).

[2] Doutt (1942, p. 93 and pl. 10) gave five measurements and a sketch of this skull from California Museum of Vertebrate Zoology. Bee and Hall (1956, p. 223–224) gave sketches.

[3] U.S. Fish and Wildlife Service, Marine Mammal Research, Seattle ; skull broken ; from Francis H. Fay.

[4] Skull slightly broken ; reconstructed (Naumov and Smirnov, 1936, p. 174–175).

[5] Puget Sound Museum of Natural History, Tacoma ; skull from Francis H. Fay.

[6] U.S. Fish and Wildlife Service, Marine Mammal Research, Seattle ; skull with abnormal dentition ; from Francis H. Fay.

[7] Naumov and Smirnov (*op. cit.*).

[8] U.S. National Museum ; skull broken ; the smaller of the two specimens measured by Doutt (*op. cit.*).

22995, with CBL 194 mm. and MW 127 mm. This skull has been mislaid.

The following seem to be reliable body measurements :

Large males : Length 168 cm. (Von Schrenk, 1859, *fide* Mohr, 1951, p. 188). Naumov (1941, p. 48) measured a male of 163 cm., and Wilke (1954, p. 221) measured one of 161 cm., weight 94·8 kg. Tanned pelts vary greatly in length from nose to tip of tail. The lengths of four adult male pelts are (cm.) : 130, 140, 155 and 156. The pelt measuring 140 cm. is from seal BDM 543, an individual whose skull is one of the largest.

Large females : length 170 cm. (Naumov, 1941; two out of five alike). Weight 78·9 kg. (174 lb.) (Wilke's specimen of 161 cm.).

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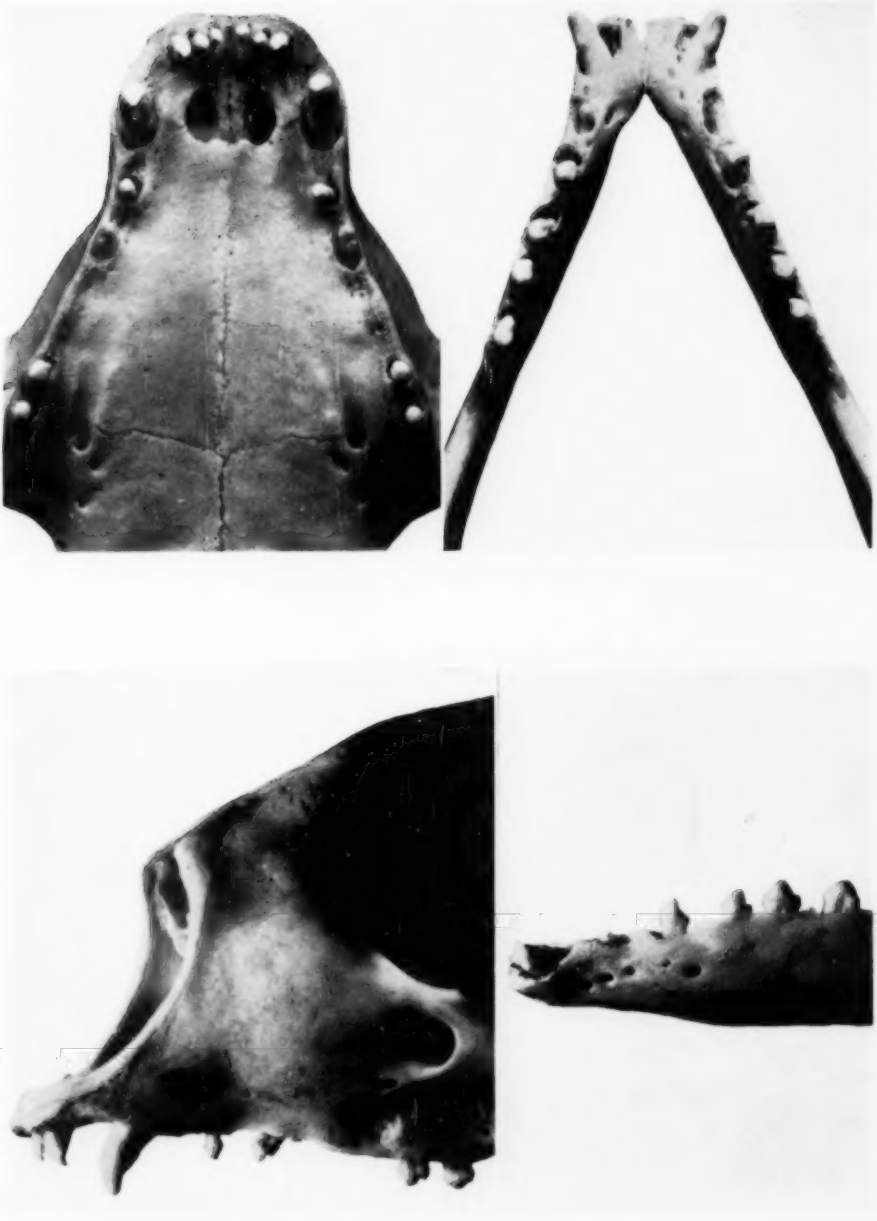
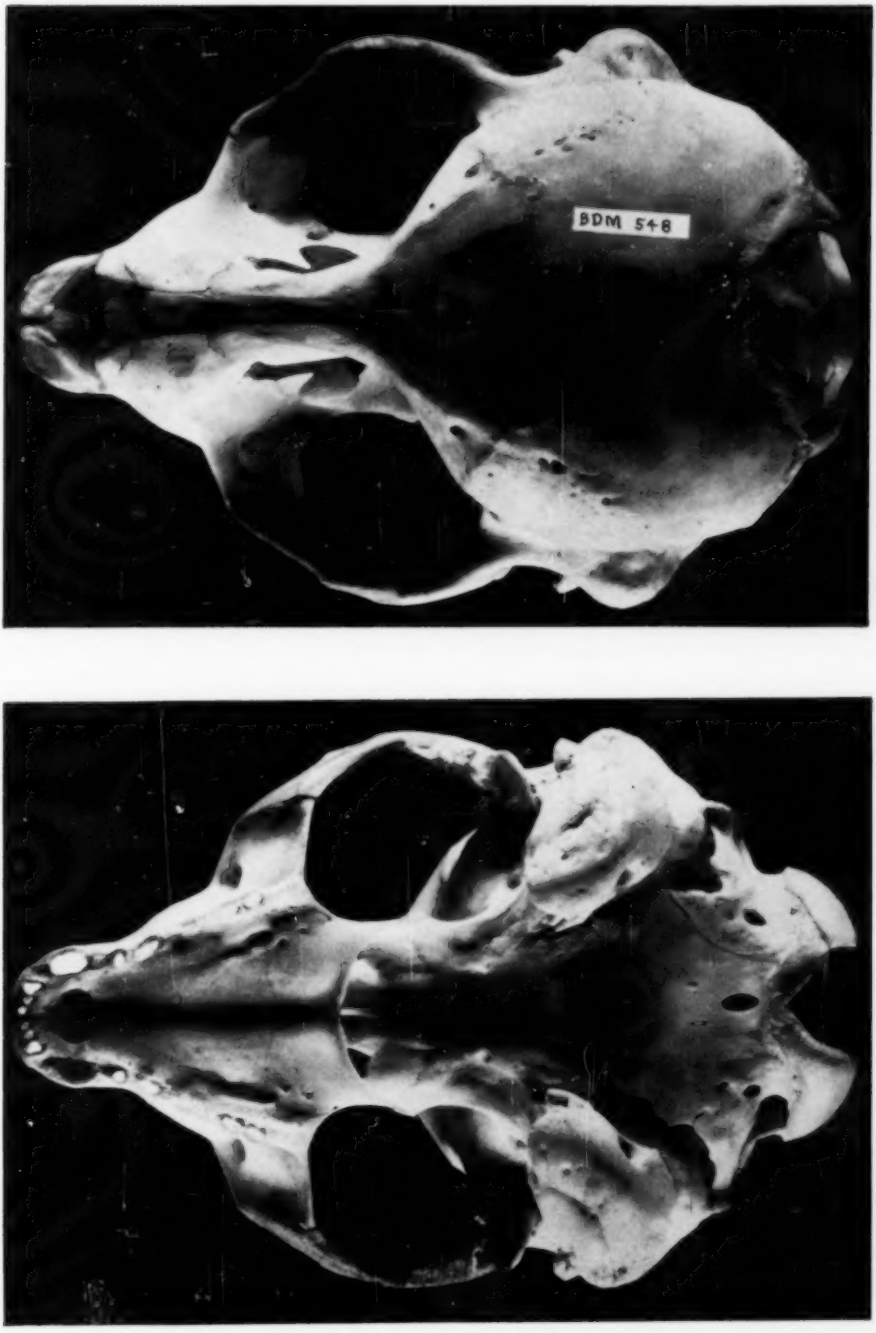
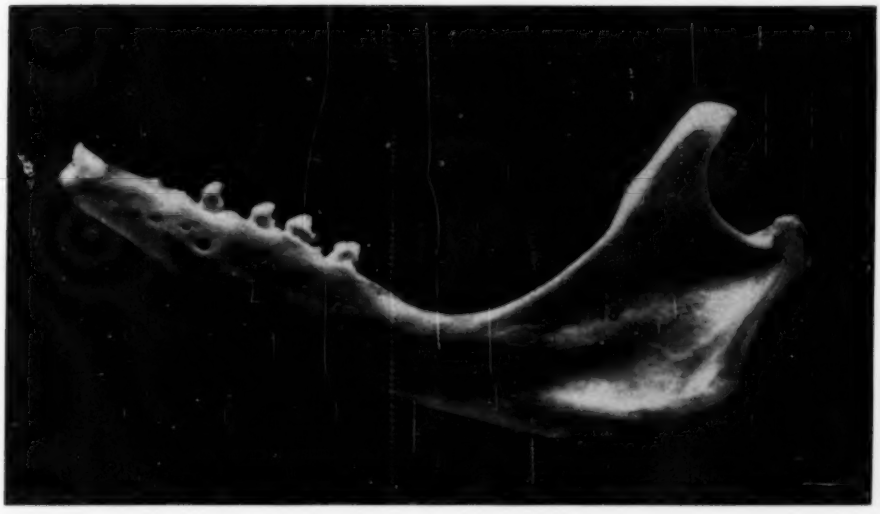


Dentition of adult male ribbon seal; specimen BDM 548.



Dentition of adult male ribbon seal; specimen BDM 548.



Dentition of adult male ribbon seal; specimen BDM 548; skull $\frac{2}{3}$ natural size; lower jaw natural size.

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COMMUNICATIONS BETWEEN THE FACIAL AND TRIGEMINAL NERVES IN CERTAIN MAMMALS

BY

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(With 1 plate and 21 figures in the text)

The modes of division and branching of the extrapetrous part of the facial nerve and the presence or absence of communications between its branches and between it and the trigeminal nerve and cervical plexus were studied in nineteen mammalian species. Communications between the facial and derivatives of the mandibular division of the trigeminal were found invariably, but were inconstant in the case of the two other divisions and of the cervical plexus.

The possible functional significance of the observations is discussed.

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INTRODUCTION

Communications between the extra-petrous branches of the facial nerve and branches of the trigeminal in man were described by Sir Charles Bell (1821, 1830) who also demonstrated their presence in the ass and monkey. After experiments in the ass he concluded that the seventh nerve was the motor nerve to muscles of facial expression and that the fifth took no part in their innervation, but supplied overlying skin. Hirschfeld & Léveillé (1866) illustrated the plexiform arrangement of the branches of the facial nerve in man ; they depicted stout communications from all three divisions of the trigeminal as well as from the great auricular and transverse cervical nerves, and maintained that all the branches of these nerves were recognizable and separable to their terminations. After reviewing the literature they agreed with Bell's interpretation of the relations and functions of the two cranial nerves, and subsequently they have been supported by others, including Frohse (1895), Hovelacque (1927), Huber (1930) and O'Connell (1936). The

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significance of these interneural communications is not fully understood but Woollard (1925), in a study of the anatomy of *Tarsius spectrum*, suggested that they represented the third and highest stage in the evolution of the distribution of the facial nerve in the first stage of which branching of the facial nerve was simple, in the second plexiform and in the third there was an additional plexiform arrangement with the trigeminal. He considered that in *Tarsius* the second stage had been reached for " It makes no plexus with the Trigeminus". Le Gros Clark (1926) reported that there were no communications between the seventh and fifth nerves in the Pen-tailed tree-shrew, although there was one between the spinal accessory and branches of the cervical plexus. However, in an exhaustive review on the evolution of facial musculature Huber (1930) stated that communications between the facial and trigeminal nerves were present in all mammalian types, particularly in regions underlying tactile vibrissae. On the basis of careful dissections he, and later O'Connell (1936), supported the classical view that fibres of the two nerves did not intermingle and that the trigeminal supplied skin, its appendages and possibly blood vessels. Recently, in a study of the variations in the maxillary nerve in primates Ashton & Oxnard (1958) suggested that the branches of the nerve " which fasciculated with twigs of the facial nerve ", might convey proprioceptive impulses from the facial muscles.

Recent histological studies in the rabbit (Bowden & Mahran, 1956, and 1960) partially supported the earlier authors, for trigeminal nerve fibres were traced to overlying skin, vibrissae and blood vessels. However, there was unequivocal evidence that bundles and fibres of the two nerves intermingled in the common nerve trunk and also they were followed into the m. quadratus labii superioris and buccinator. The myelinated fibres of the main seventh nerve trunk measured from 1–12 μ in diameter and those from the trigeminal which entered the former muscle ranged from 1–22 μ. The precise distribution of the largest fibres is not wholly clear, but it is of interest to note that fibres measuring 15–20 μ were found to supply annúlo-spiral endings in three muscle spindles in m. quadratus labii superioris of this animal (Bowden & Mahran, 1956 and 1960). Spindles and other sensory endings have now been found in facial muscles in man (Kadanoff, 1956) and the source of their afferent innervation is also unknown, although clinical evidence can be marshalled in support of each of two hypotheses, one suggesting its origin from the trigeminal and the other from the facial nerve (see Mahran, 1955, for review of literature). Further experimental investigation is called for, and since the size frequency distribution of fibres in the main facial nerve trunk indicated that in the rhesus monkey, cat and rabbit, this nerve was unlikely to supply the sensory fibres to classical spindles (Wakeley & Edgeworth, 1933 ; Foley & Dubois, 1943 ; Bruesch, 1944 ; Bowden & Mahran, 1960), the communications between it and the trigeminal assumed an added interest and importance.

The results reported here form part of an investigation into the afferent supply of the mimetic muscles. Although gross dissection alone could offer no solution to the problem, it was an essential preliminary to any experimental study, for no information appeared available for the rabbit, and there were

few details and some significant discrepancies in the accounts of the distribution of the facial nerve and of its communications with the trigeminal in the cat and dog (Mivart, 1881 ; Reighard & Jennings, 1940 ; Taylor & Weber, 1951 ; Davison, 1952 ; and Bourdelle & Bressou, 1953). As material became available the scope of the investigation broadened to include animals which would be unsuitable or unavailable for routine experimental investigation.

MATERIALS AND METHODS

Ninety-seven facial nerves from nineteen species were studied. The number of available species and nerves in each of seven orders was as follows :

ORDER	Number of species	Number of facial nerves
Monotremata	1	2
Marsupialia	1	2
Insectivora	1	2
Chiroptera	1	2
Lagomorpha	1	32
Carnivora	3	22
Primates	11	35
	19	97

Further particulars of the material are given in Tables 1–3. Careful dissections were made, photographed and drawn. Details of the course, mode of division and distribution of the facial nerve and of the presence or absence of communications with the trigeminal nerve and branches of the cervical plexus were noted for each specimen. The details of distribution of the facial nerves will be reported elsewhere.

FINDINGS

These will be given in two parts, the first dealing with the facial nerve and communications between its branches ; the second with communications between the facial and trigeminal nerves and between the facial and the cervical plexus.

A. *The facial nerve*

Three patterns of branching were distinguished, two clear-cut and one intermediate in form. In the first the nerve pursued a linear course on the

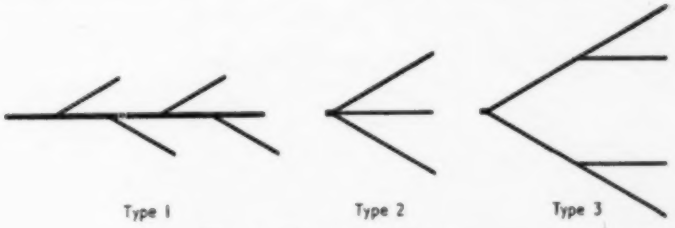

Fig. 1.—Types of facial nerve.
a. Linear arrangement of branches ; b. Fan-like branching of main trunk ; c. Main nerve trunk dividing into upper and lower divisions.

face and gave off branches in sequence ; in the second, intermediate group, branches appeared to form a fan-like spray; and in the third, the main nerve trunk divided into distinct upper and lower or temporo-facial and cervico-facial trunks after giving off the posterior auricular complex (Fig. 1). In the first group were the spiny anteater, European hedgehog and Indian fruit bat (Table 1 and Figs. 2–4), and the intermediate group consisted of four primate

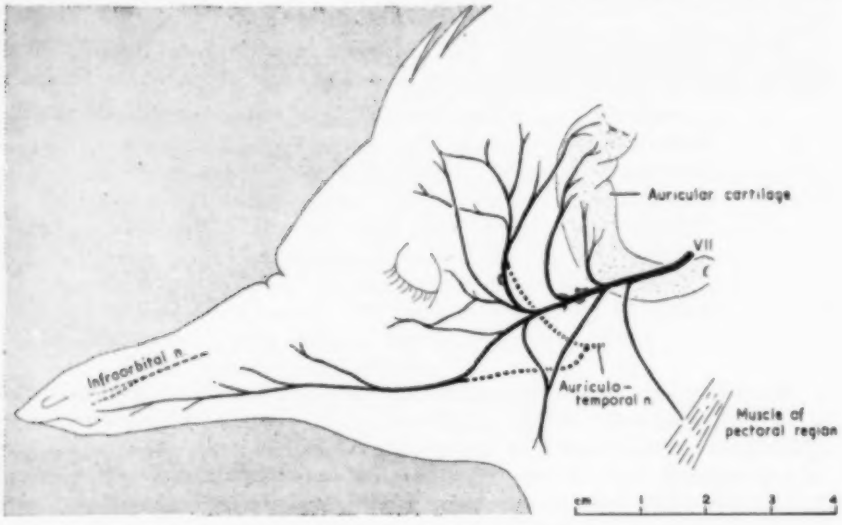

Fig. 2.—*Echidna tachyglossus*. Left side of face.
In this and all ensuing text-figures ——— = VIIth nerve ; – – – = Vth nerve.

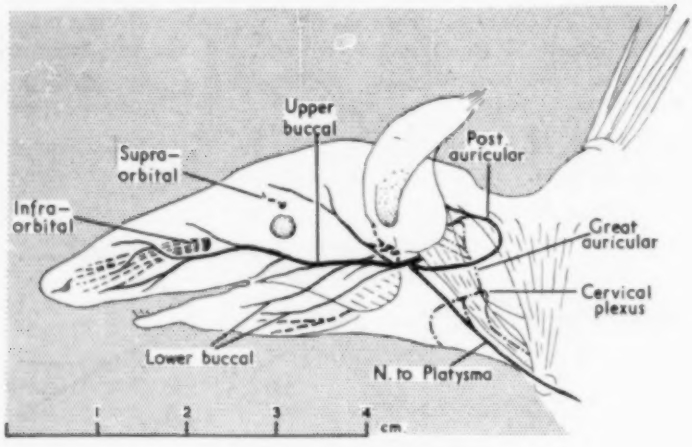

Fig. 3.—*Erinaceus europaeus*. Left side of face.
——— · ——— · ——— = branches of cervical plexus.

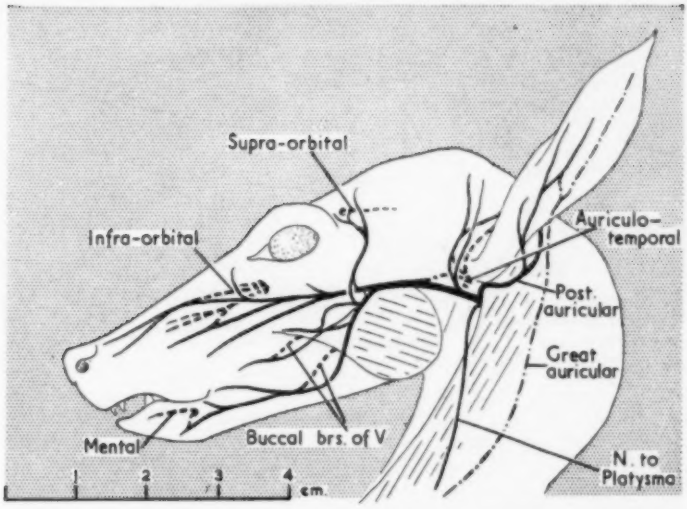

Fig. 4.—*Pteropus giganteus*. Left side of face.

species, the tree-shrew, common potto, tarsier and black pencilled marmoset (Table 2 and Figs. 5–8). The third and largest group consisted of the ursine wombat (Fig. 9) rabbit (Fig. 10), cat, dog, grey seal, white collared mangabey, tantalus monkey, sacred baboon, lar gibbon, orang-utan, chimpanzee and man (Table 3 & Figs. 11–21). Inspection of the figures and tables shows that the

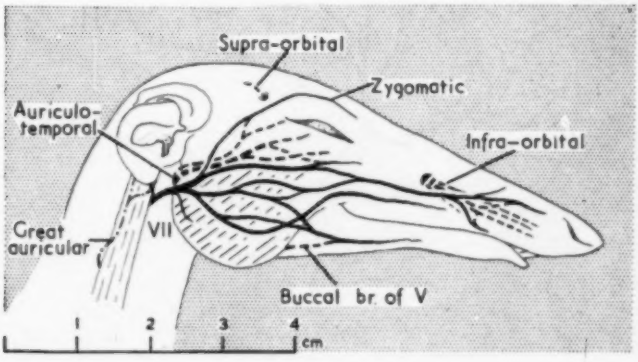

Fig. 5.—*Tupaia tana*. Right side of face.

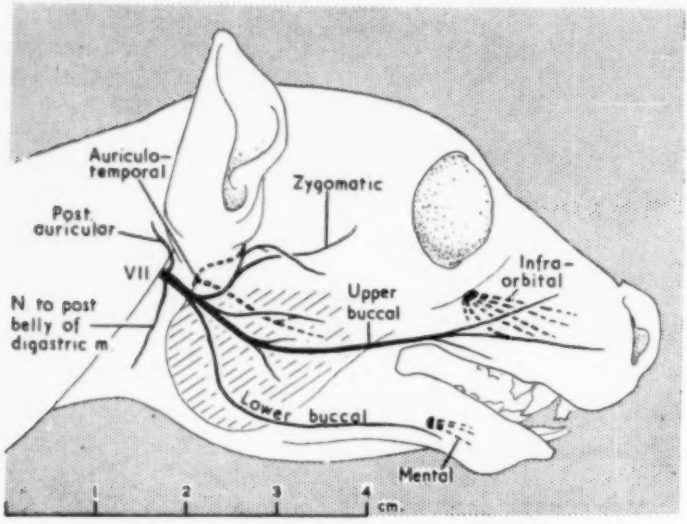

Fig. 6.—*Perodicticus potto*. Right side of face.

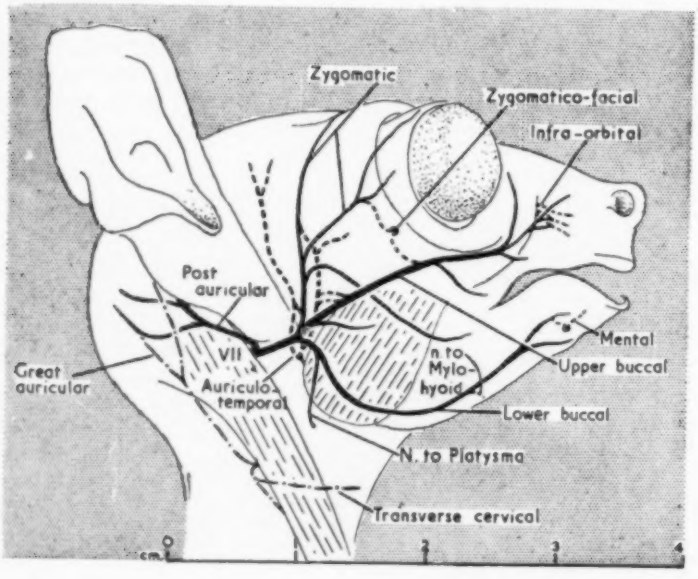

Fig. 7.—*Tarsius spectrum*. Right side of face.

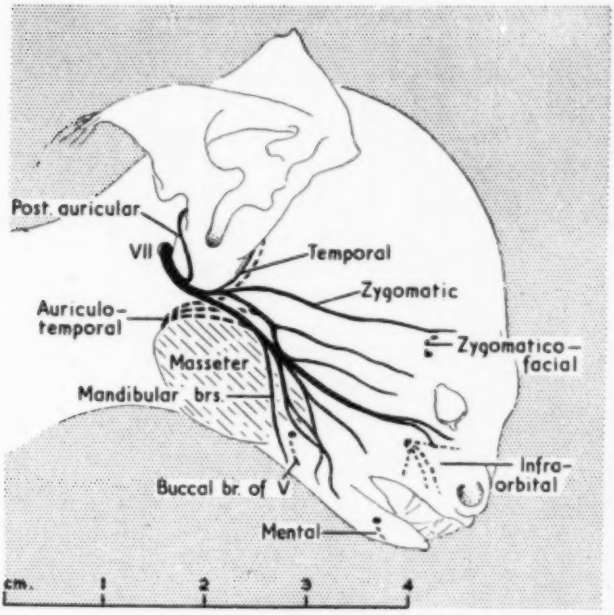

Fig. 8.—*Hapale penicillata*. Right side of face.

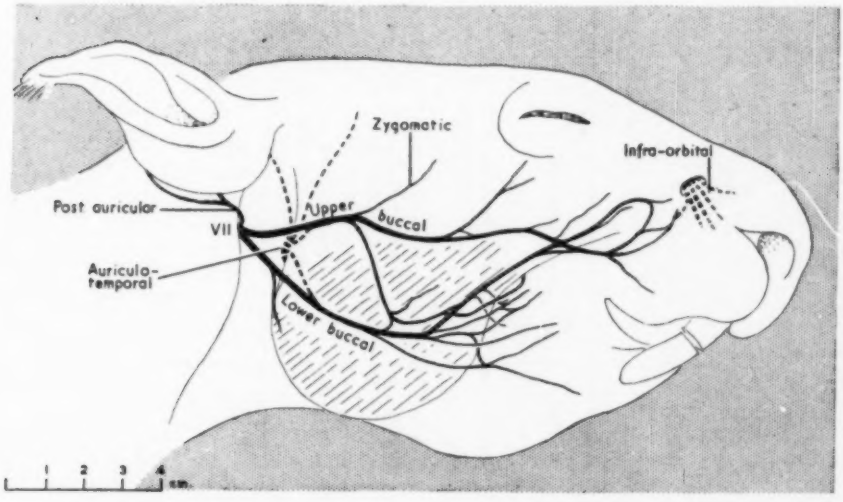

Fig. 9.—*Phascolomis ursinus*. Right side of face.

TABLE 1

VIIth nerve with single main trunk and branches in linear sequence.

Order	Species	No. of nerves examined	Type of branching	Communications between branches of facial nerves No. of participating branches
Monotremata	*Echidna tachyglossus* Spiny anteater (Fig. 2)	2	S.	3. i. Terminals in supra orbital region ii. Terminals in infra orbital region iii. Branches to platysma
Insectivora	*Erinaceus europaeus* Hedgehog (Fig. 3)	2	S.	
Chiroptera	*Pteropus giganteus* Indian fruit bat (Fig. 4)	2	C.	2. i. Terminals in supra orbital region ii. Branches of lower buccal nerve

S. = simple. C. = complex.

TABLE 2

VIIth nerve trunk dividing into spray of terminal branches.

Order	Species	No. of nerves examined	Type of branching	Communications between branches of VIIth							
				No.	Participating branches						
					P.A.	T.	Z. & U.B.	U.B.	U. & L.B.	L.B.	C.
Primates	*Tupaia tana* Tree-shrew (Fig. 5)	2	C.	3				+	+	+	
	Perodicticus potto Common potto (Fig. 6)	4	S.	1 var.					2/4+		
	Tarsius spectrum Tarsier (Fig. 7)	2	S.	1			+				
	Hapale penicillata Black-pencilled marmoset (Fig. 8)	4	S.	2			+			+	

P.A. = post-auricular
T. = temporal
Z. = zygomatic
U.B. = upper buccal
L.B. = lower buccal
C. = cervical

Branches of VII

S. = simple.
C. = complex.

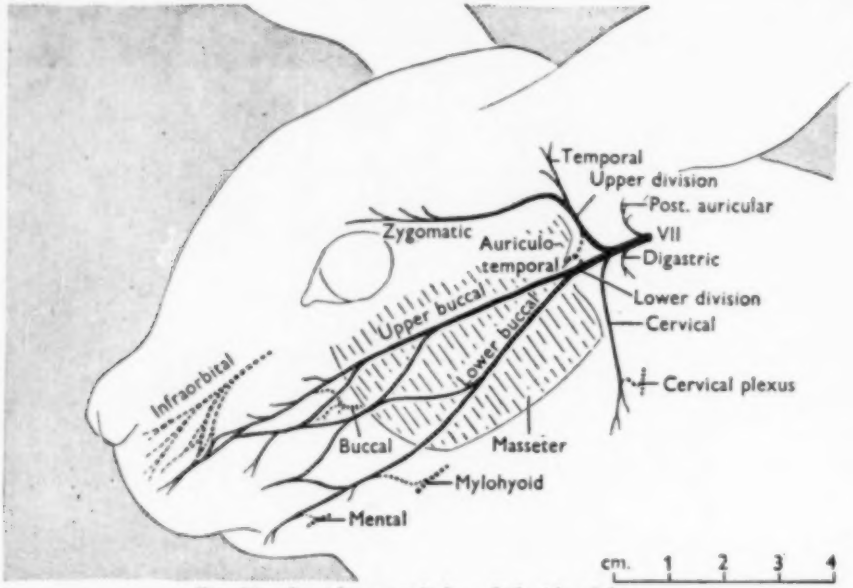

Fig. 10.—*Oryctolagus cuniculus*. Left side of face.

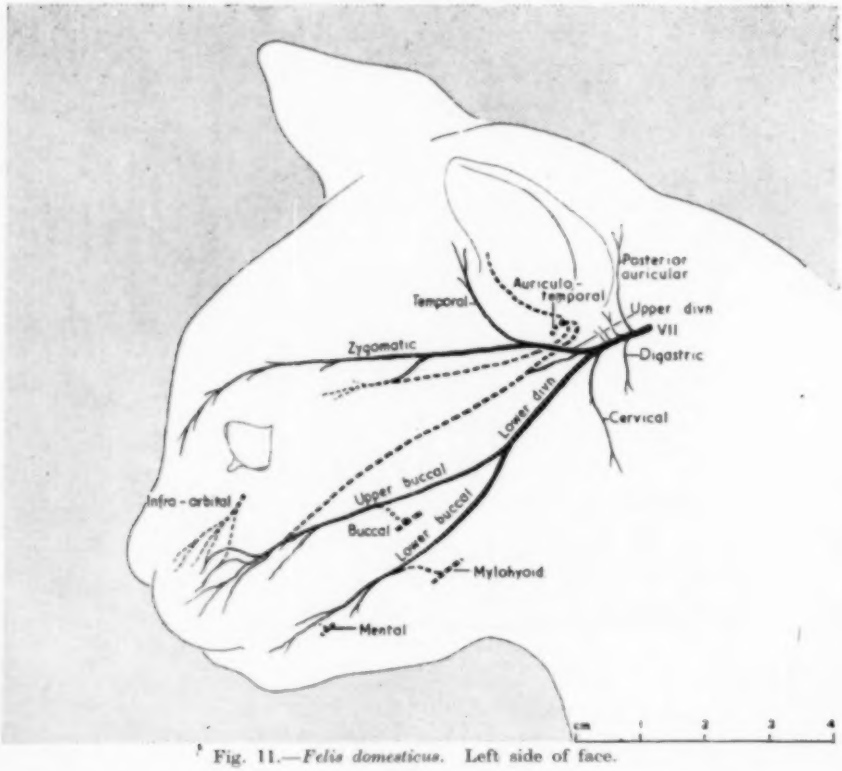

Fig. 11.—*Felis domesticus*. Left side of face.

terminal branches might either be simple or complex, and examples of each type were found in the three main groups. The carnivora (cat, dog, seal, Figs. 11–14) had distinct upper and lower main divisions and terminal branching was simple, except for a variable complexity of arrangement in the auricular region of the seal. Minor variations in branching were found in the four nerves of the two dogs, whilst in the seven cats the pattern was remarkably constant. Primates were found in the second and third groups in this series. Branching was simple in the potto, tarsier, black pencilled marmoset, white collared mangabey and tantalus monkey (Figs. 15 and 16) and complex in the tree shrew, sacred baboon (Fig. 17), lar gibbon, the available parts of the orang-utan and the single chimpanzee nerve (Figs. 18 and 19). In man the branching was most elaborate, more so in the adult than in the foetus (*cf.* Figs. 20 and 21).

No communications were found between branches of the facial nerve in the hedgehog, one of two pottos and the cat (Figs. 3, 6 and 11). In the spiny anteater, Indian fruit bat, white collared mangabey and tantalus monkey, communications were confined to terminal branches, and sometimes to

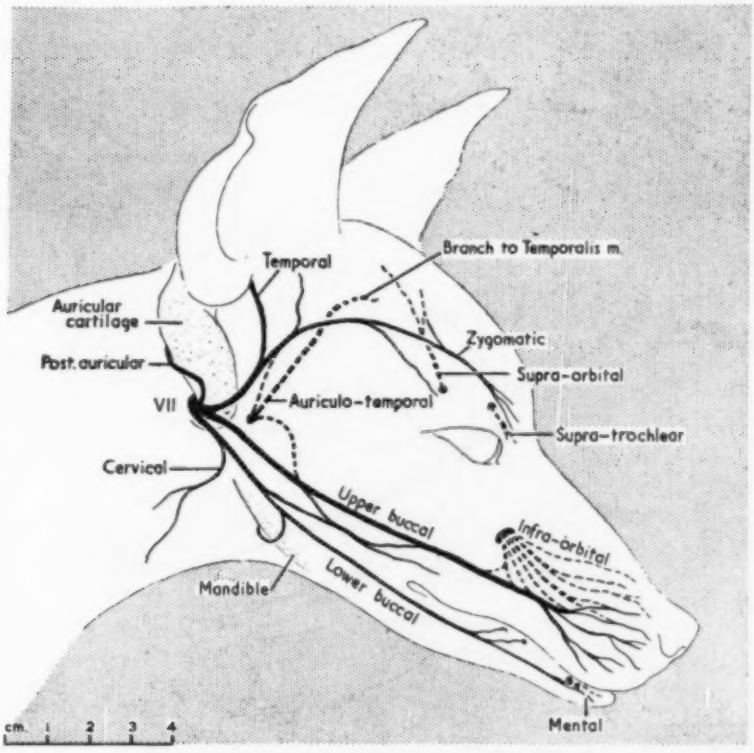

Fig. 12.—*Canis familiaris*. Right side of face.

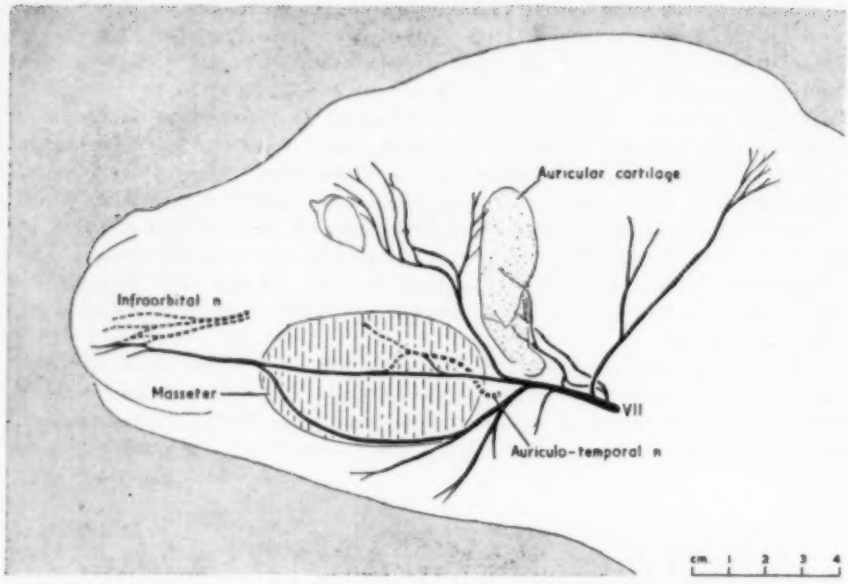

Fig. 13.—*Halichoerus grypus*. Left side of face of pup.

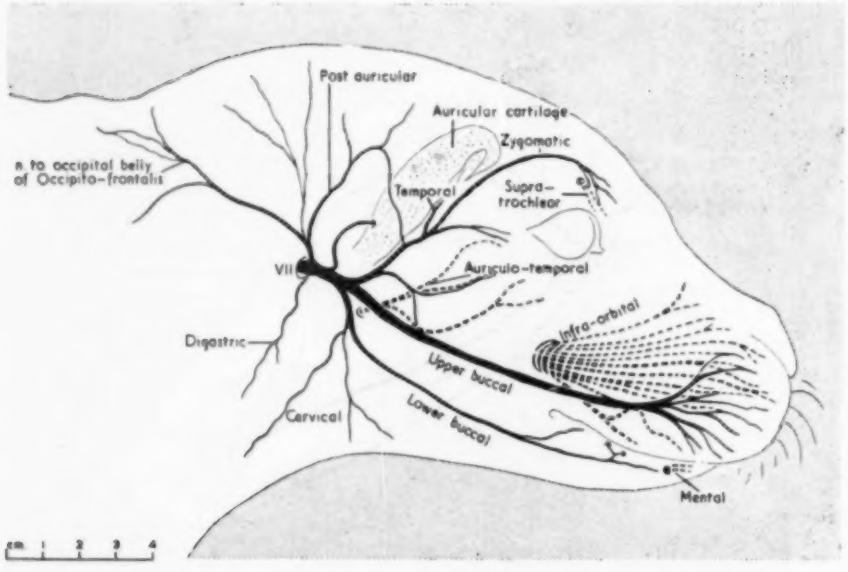

Fig. 14.—*Phoca*. Right side of face of adult.

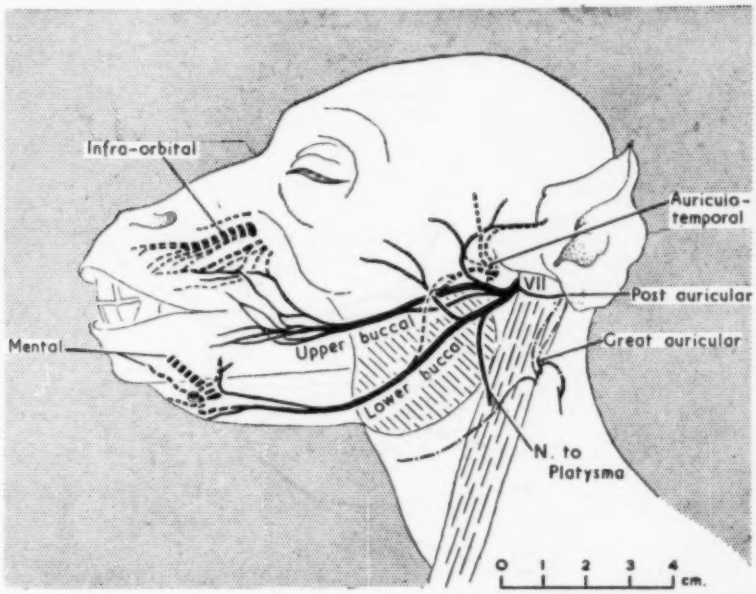

Fig. 15.—*Cercocebus collaris*. Left side of face.

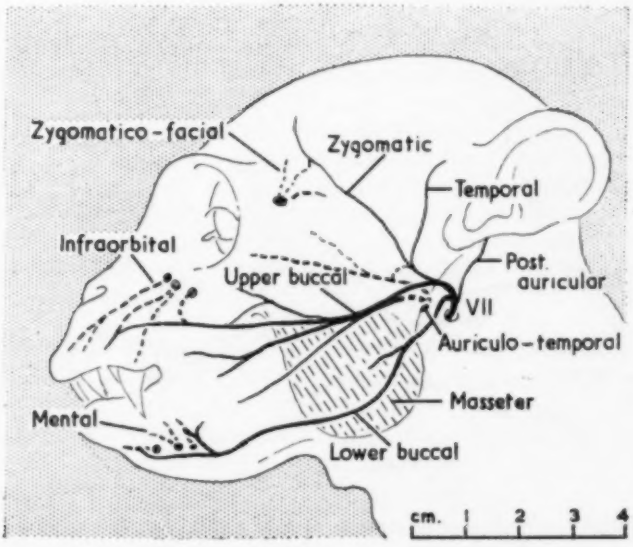

Fig. 16.—*Cercopithecus tantalus*. Left side of face.

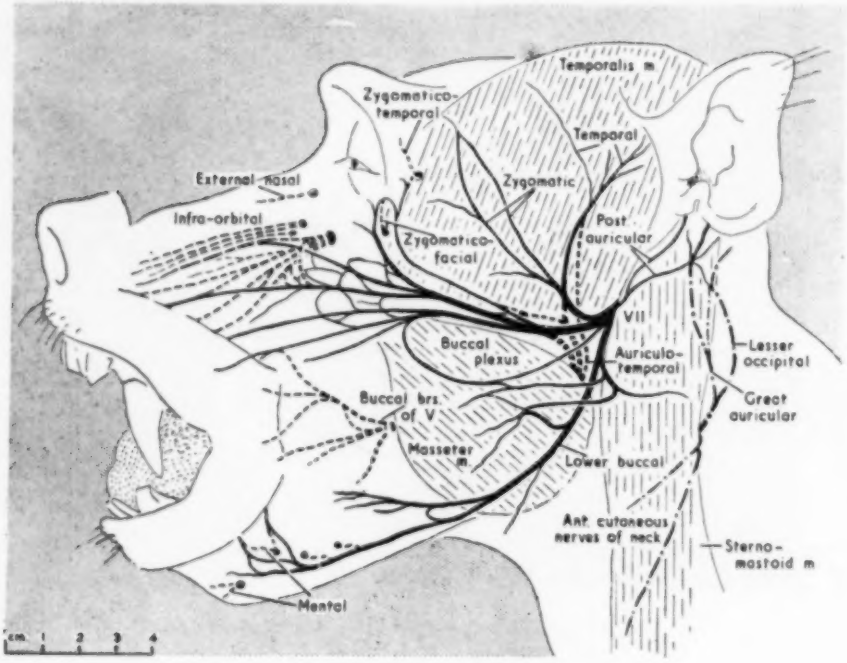

Fig. 17.—*Papio hamadryas*. Left side of face.

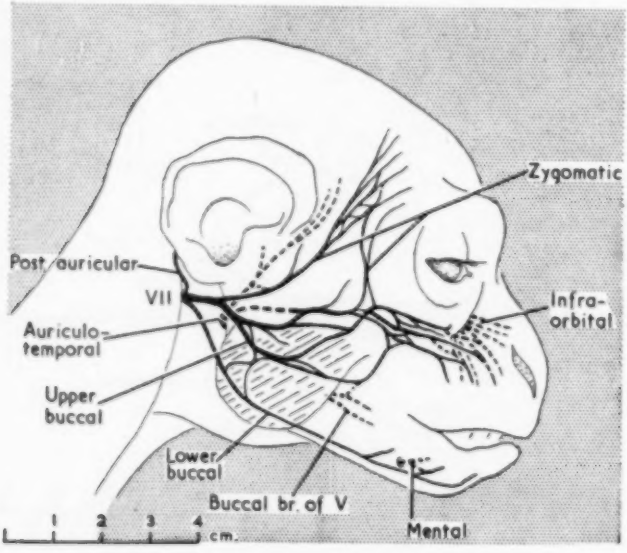

Fig. 18.—*Hylobates lar*. Right side of face.

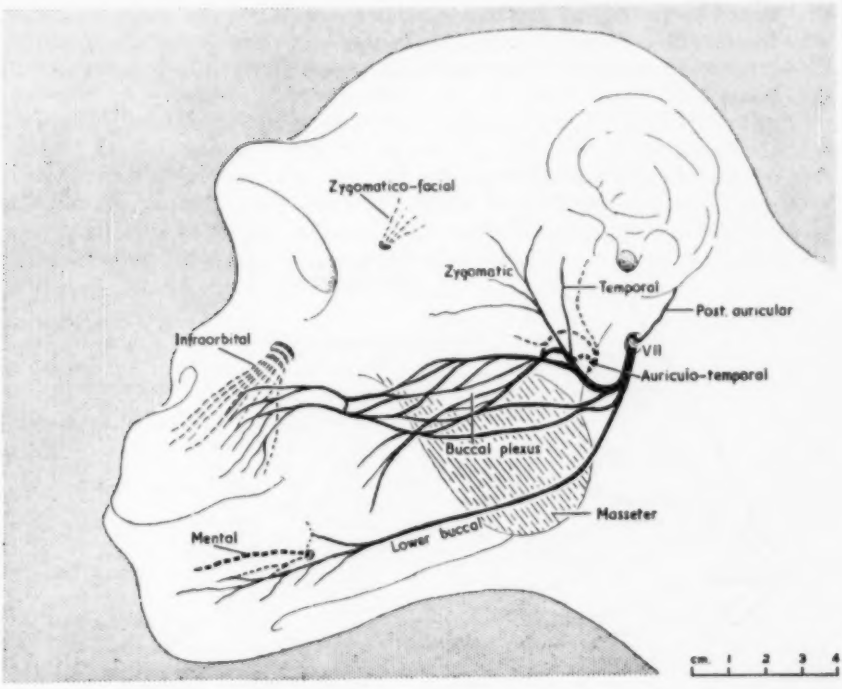

Fig. 19.—*Pan troglodytes*. Left side of face.

terminals of a single branch of the main nerve trunk (Figs. 2, 4, 15 and 16). In the remaining animals of Groups II and III more proximal communications occurred and the incidence of plexus formation between neighbouring branches was greater, particularly in the Hominoidea. Of the sixteen species in which communications occurred, ten had circumoral communications between the upper and lower buccal branches (there was insufficient material to examine these in the orang-utan) and in six there were communications between the zygomatic and upper buccal branches of the facial nerves. In man communications occurred between all branches.

B. *Communication between seventh and fifth nerves*

(i) *Ophthalmic division of Vth Nerve*. Delicate communications were found between the two cranial nerves in the Indian fruit bat and tarsier (Figs. 4 and 7) and in the rabbit they were only found in the substance of the orbicularis oculi. Inconstant communications were found in the dog, grey seal and tantalus monkey (Tables 4 and 5).

(ii) *Maxillary division of Vth Nerve*. Communications were found between branches of the facial and the maxillary division in all but the spiny anteater ; in the wombat none was found on the left side and only one communication

was present on the right. In the remaining species numerous communications were found (Plate 1, figs. 1, 2 and 3) and an elaborate plexus was found in man, the components of which were not separable by dissection (Plate 1, figs. 4 and 5).

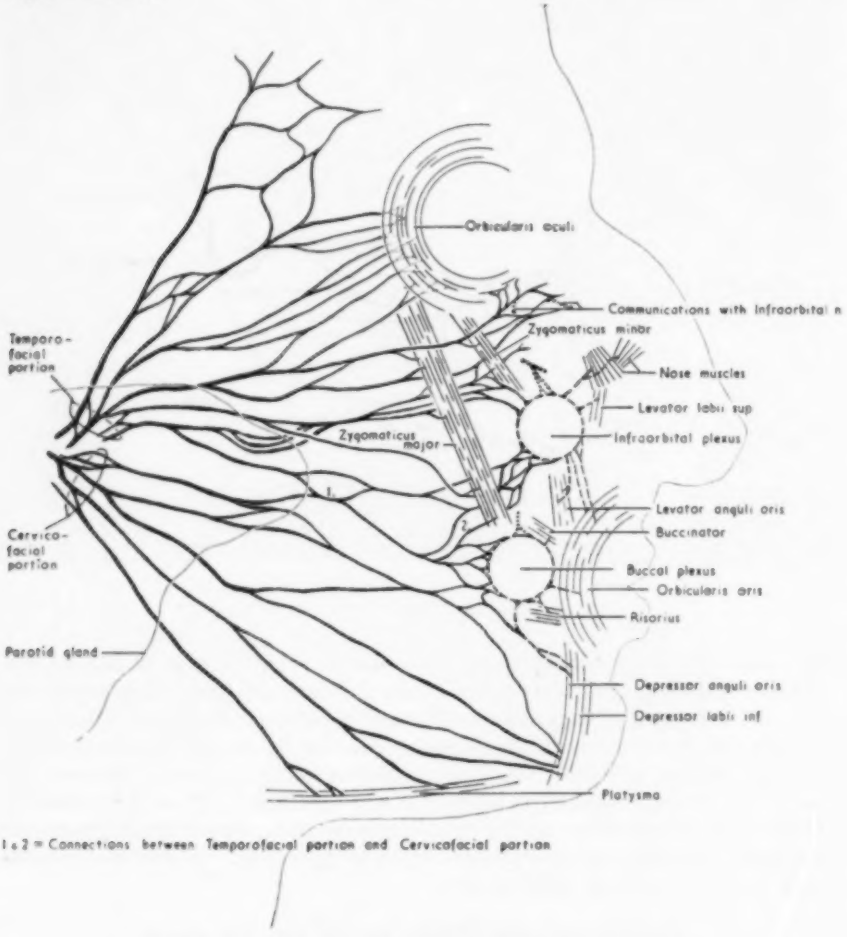

Fig. 20.—*Homo sapiens* branching of right facial nerve in an adult.

(iii) *Mandibular division of Vth Nerve.* Communications were found in all specimens except the orang-utan where there was insufficient material to examine this point (Tables 4 and 5). With this exception, communications with the auriculotemporal nerve were invariable and might be simple or plexiform (Plate 1, figs. 6, 7 and 8). Other branches of the third division of the trigeminal which communicated with the facial were the buccal in the Indian fruit bat, tree-shrew (Plate 1, fig. 7), one of the two pottos, rabbit,

cat, sacred baboon, lar gibbon and man (Plate 1, figs. 4, 5 and 9), and the nerve to mylohyoid in the fruit bat, one potto, tarsier (Plate 1, fig. 10), marmoset, rabbit, cat, dog, mangabey, tantalus monkey, baboon, gibbon, chimpanzee and man. These communications were invariably distal to the point at which the posterior auricular branches were given off the main nerve trunk ; in the cat they mostly reached the seventh nerve branches in the anterior half of the face (Fig. 11). In one potto there appeared to be no communication between the trigeminal and the lower buccal branch of the facial nerve, and one of two branches of this nerve in the hedgehog was given off before the auriculotemporal communication (the sole one from the mandibular division) reached the facial nerve (Fig. 3).

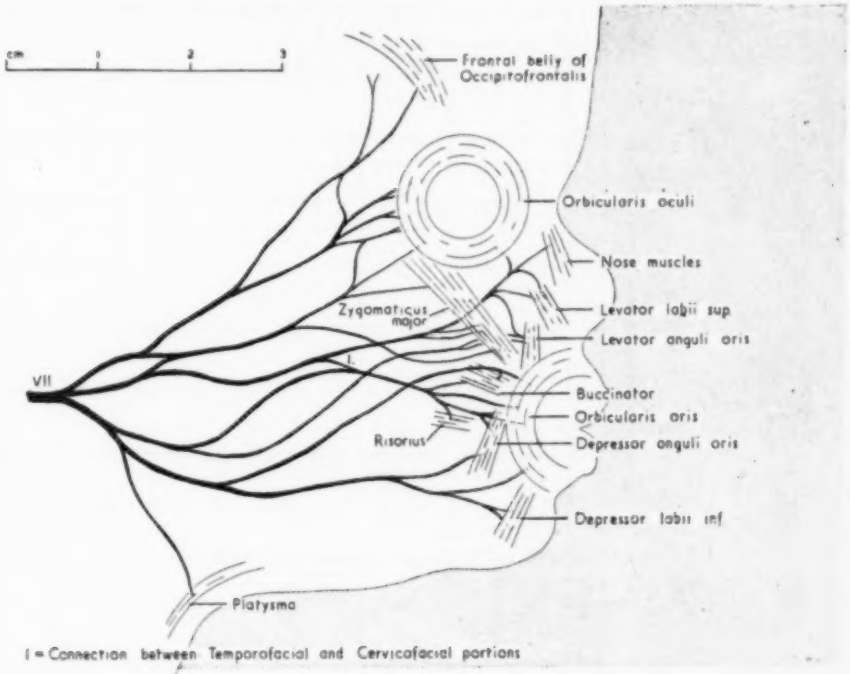

Fig. 21.—*Homo sapiens* branching of right facial nerve in a full term foetus.

Communications between the facial nerve and Cervical plexus (Table 4). Free communications were found in the European hedgehog, Indian fruit bat and tree-shrew (Figs. 3, 4 and 5) ; no communications were found in potto, tarsier, black pencilled marmoset, ursine wombat, grey seal, white collared mangabey, tantalus monkey and chimpanzee. Variable communications were found in the dog and sacred baboon. In man and cat either no communications were found, or very fine ones were traced out in the substance of platysma. There was insufficient material to investigate this point in the spiny anteater and orang-utan.

TABLE 3

VIIth nerve with upper and lower divisions.

Order	Species	No. of nerves examined	Type of branching	Communications between branches of VIIth										
				No.	Main U. and L. Div.	P.A.	P.A./T.	T.	T./Z.	Z.	Z./U.B.	U.B.	U.B./L.B.	L.B.	L.B./C.
Marsupialia	*Phascolomis. Ursinus* Ursine wombat (Fig. 9)	2	S./C. distally	4	+							+	+	+	
Lagomorpha	*Oryctolagus cuniculus* Rabbit (Fig. 10)	32	S.	1									+ simple plexus		
Carnivora	*Felis domesticus* Domestic cat (Fig. 11)	14	S.												
	Canis familiaris Dog (Fig. 12)	4	S.	1									+		
	Halichoerus grypus Gray seal pup (Fig. 13)	4	S. face	3. var.			3/5+				3/5+		3/5+		
	Phoca adult (Fig. 14)	1	C. in aurcular region												

Primates	*Cercocebus collaris* White-collared mangabey (Fig. 15)	2	S.	1								+			
	Cercopithecus tantalus Tantalus monkey (Fig. 16)	2	S.	1								+			
	Papio hamadryas Sacred baboon (Fig. 17)	2	C.	5	+				+	(2)		+ plexus	+	+	
	Hylobates lar Lar gibbon (Fig. 18)	2	C.	mult.				.....	.....	..plexiform		.....	.....		
	Pongo pygmaeus Orang-utan	part of 1	C.	mult.	N.A.			.....	.....	plexiform		.....	N.A.	N.A.	N.A.
	Pan troglodytes Chimpanzee (Fig. 19)	1	C.	mult.				.....	.....	..plexiform		.....	+		
	Homo sapiens Man (adult) (Fig. 20) (foetus) (Fig. 21)	10 2	C. less C.	mult.				.....	.....	.....	..plexiform	.....	.....	.....	.....

N.A. = not available.

TABLE 4

Communications between the VIIth and Vth nerves and between VIIth and cervical plexus.

Type of facial nerve		Divisions of Trigeminal			Cervical Plexus	
		V_1	V_2	V_3	G.A.	A.C.
Single trunk	Spiny anteater			+	—N.A.—	
	European hedgehog		+	+	+	+
	Indian fruit bat	+	+	+	+	+
Fan branches	Tree-shrew		+	+	+	
	Potto		+	+		
	Tarsier	+	+	+		
	Black-pencilled marmoset		+	+		
Upper and lower divisions	Ursine wombat		1/2+	+		
	Rabbit	+	+	+	+	
	Cat		+	+	In platysma	+
	Dog	+var.	+	+		2/4+
	Gray seal	+var.	+	+		
	White-collared mangabey		+	+		
	Tantalus monkey	+var.	+	+		
	Sacred baboon		+	+	1/2+	
	Lar gibbon		+	+		
	Orang-utan		+	N.A.	—N.A.—	
	Chimpanzee		+	+		
	Man		+	+	o or v. fine	

N.A. = not available. Var. = variable. G.A. = great auricular nerve.
Divisions of trigeminal designated V_1, V_2, V_3. A.C. = anterior cutaneous nerve of neck.

DISCUSSION

Single specimens only were available for ten species and only the left side and part of the left half of the face were available for the chimpanzee and orang-utan respectively. The tissues were so indurated and brittle in the chimpanzee and one potto, that significance can only be given to positive findings in these two specimens. In spite of these limitations, certain interesting points emerged from the observations.

It is clear that the arbitrary grouping based on the form of branching of the main facial nerve trunk has no taxonomic significance, for the marsupial ursine wombat and the higher primates including man, were found together in the third group with one lagomorph and three species of carnivore, whilst other primates were in the second group. The anatomical arrangement of the pre-auricular branches of the main trunk appears to be roughly, but not precisely, correlated with the form of the face. The three animals in the first group, with a single main trunk which gave off branches in linear sequence, had long pointed snouts (Figs. 2–4), but on the other hand, animals with the same type of facial configuration, such as the tree-shrew (Fig. 5), and the two dogs studied here (Fig. 12), were in the second and third groups respectively.

TABLE 5

Branches of the Vth nerve communicating with VIIth.

	V_1		V_2			V_3			
	S.O.	S.T.	Z.T.	Z.F.	I.O.	A.T.	B.	N. to M.	M.
Spiny anteater						+			
European hedgehog					+	+			
Indian fruit bat	+				+	+	+		+
Tree shrew					+	+	+		
Potto					+	+	2/4+		2/4+
Tarsier				+	+	+			+
Black-pencilled marmoset					+	+			+
Ursine wombat					1/2+	+			
Rabbit	*+				+	+	+	+	+
Cat					+	+	+	+	+
Dog	2/4+			1/4+	+	+		+	+
Grey seal		3/5+			+	+			3/5+
White-collared mangabey					+	+			+
Tantalus monkey	1/2+			1/2+	+	+			+
Sacred baboon			+	+	+	+	+		+
Lar gibbon					+	+	+		+
Orang-utan					+	N.A.	N.A.	N.A.	N.A.
Chimpanzee					+	+			+
Man					+	+	+		+

V_1 { S.O. = supra orbital. S.T. = supra trochlear.

V_2 { Z.T. = zygomaticotemporal. Z.F. = zygomaticofacial. I.O. = infra orbital

V_3 { A.T. = auriculotemporal. B. = buccal nerve. N. to M. = nerve to mylohyoid. M. = mental nerve.

* Fine communication in orbicularis oculi.

According to Woollard (1925), the criteria by which three stages in the evolution of the distribution of the facial nerve could be recognized were as follows : branches of the nerve were simple in the first, plexiform in the second, and in the third they communicated with the trigeminal nerve. Examples of simple and complex branching of the facial nerve were found in the Primates (Tables 2 and 3), and whilst the complexity was greatest in the Hominoidea (Figs. 18–21 inclusive), plexiform branching was also seen in *Tupaia* (Fig. 5), the anterior half of the face of the ursine wombat (Fig. 9) and was variable in the auricular region of the seal (Fig. 14). The pattern of branching was strikingly uniform in the seven cats ; but the details of terminal branching varied between individuals and between the two sides of a single individual in the seal, dog, and in man, where they were most striking. Variations in the topography of the cervical branch and their surgical significance in man have been discussed by Lagrot (1924).

In this series, communications between branches of the seventh nerve were found in all animals except the single European hedgehog, the seven cats and one of two pottos. In the remainder, they varied in number (Tables 1, 2 and 3) ; where sparse they tended to be found between branches supplying the muscles of the lips, and they were increasingly numerous in the sacred baboon, anthropoid apes and in man where they were most intricate and generalized in distribution. When the human foetus and adult are compared (Figs. 20 and 21), it will be seen that the pattern is more complex in the latter, a phenomenon almost certainly related to the growth of the face which would tend to draw out and separate the strands of a loose intraneural plexus. Evidence that growth can alter the spatial relationships of the nerve is provided by the fact that the angle between the main upper and lower divisions is acute in the child and obtuse in the adult (Bockenheimer, 1904, 1906 ; Hovelacque 1927).

Turning next to the communications between the facial and trigeminal nerves, the observations made here on Tarsius were at variance with those of Woollard (1925) but confirmed Huber's general statement that such communications invariably exist in the mammalian face. Comparison between Fig. 7: Plate 1, fig. 8 and Fig. 44, in Woollard's paper, reveals a remarkable similarity in the appearance of the gross pattern of innervation. Although branches of the seventh nerve were simple and not plexiform in our specimen, simple plexuses (in the positions indicated by Wollard) were formed at the sites of communication with the auriculotemporal and zygomatico-facial nerves. Since the stems of the two latter nerves are not only slender but also approach at an angle from a deeper plane, it is possible that they may have been overlooked in the earlier study. Derivatives of the third or mandibular division of the trigeminal nerve invariably communicated by one or more branches with the facial nerve at sites distal to the posterior auricular nerve. In every case, except the orang-utan where there was insufficient material, the auriculotemporal nerve communicated with the facial (Table 5). The source of the maxillary communications (absent only in the spiny anteater and on one side of the ursine wombat) also varied, as might be expected from Oxnard's findings in the Ceboidea (1957). The general paucity of communications with the ophthalmic division of the trigeminal and the inconstancy of those with the cervical plexus are difficult to reconcile with previous reports. No trace was found of the stout branches depicted by Hirschfeld & Léveillé (1866) in man and errors of dissection and observation cannot be excluded from our study.

Whilst the details of Woollard's hypothesis received no support, there was evidence that the complexity of the gross pattern of innervation increased with ascent of the phylogenetic scale, reaching a maximum in man. Huber (1930) correlated similar observations with the increasing differentiation of the mimetic musculature—which, in turn, is related to an increasing range and variation of facial expression most evident in the Hominoidea—and it is of interest to consider further the possible significance of the anatomical arrangements in the peripheral distribution of these two cranial nerves. The presence of communications between branches of the facial nerve might be due partly to growth changes in the face, a point already discussed, but it might also provide an anatomical pathway for branches of a single parent axon to inner-

vate diffusely scattered muscle fibres, not only within a single muscle but also within several different muscles. There is evidence of diffuse motor units in certain muscles, including those of the face (Feindel, Hinshaw & Weddell, 1952 ; Bowden & Mahran, 1956), but, as yet, there is no evidence for a diffuse intermuscular motor unit in the healthy individual. After certain injuries to the facial nerve, synkynesia, the result of misdirection and abnormal branching of regenerated fibres, demonstrates the anatomical possibility of the existence of such an intermuscular unit. It is perhaps suggestive that this plexiform arrangement of the nerve is most elaborate in man for, as well known, a single facial muscle may participate in the production of a wide range and rapidly changing variety of facial expressions, an observation which confirms the findings of Ashton & Oxnard (1958). In their series of primates they reported that this plexus was most elaborate in man " where the mimetic musculature reaches the peak of its development ", and they suggested that proprioceptive fibres might " reach the facial muscles through an enlarged zygomatico-facial nerve ".

Whilst communications between the facial and trigeminal nerves may be related to tactile vibrissae (Huber, 1930) (Plate 1, figs. 1, 2 and 3), this was not invariable ; for example, none was present in immediate relation to the luxuriant supra-orbital vibrissae of the cat and to the numerous but less conspicuous ones of the sacred baboon ; but the communications were particularly complex in the absence of vibrissae in the maxillary region of man (Plate 1, figs. 4 and 5), a finding which prompted Ashton & Oxnard to suggest the proprioceptive function of these fibres. Bowden & Mahran (1956 and 1960) demonstrated that the trigeminal fibres not only supplied blood vessels, skin and its appendages but also entered facial muscles in the rabbit. These myelinated fibres in the muscular nerves ranged from 1–22 μ in diameter, thus supplying presumptive evidence that the sensory innervation of muscle spindles is trigeminal in origin. The invariable finding of communications between the facial nerve and the mandibular division of the trigeminal in this series suggests the mandibular division is the main pathway for the afferent proprioceptive fibres. With the exception of the lowermost of the two lower buccal nerves in the European hedgehog the sites of the communications between this division and facial nerve are such that it is theoretically possible for trigeminal fibres to enter each of the terminal branches of the seventh. However, there was no evidence that this occurred in relation to the postauricular branches of the seventh in any of the species studied here. It might be suggested that afferent fibres left the auricular muscles through branches of the cervical plexus, but communications were not constantly present (Table 4), even in the dog, an animal with large and mobile ears. It is not possible to exclude errors of dissection, but afferent fibres might leave the muscles without forming communications with the facial nerve, and clearly further anatomical, histological and experimental observations are necessary.

SUMMARY

1. The modes of division and branching of the extrapetrous parts of the facial nerve, and the presence or absence of communications between its

branches, and between it and the trigeminal nerve and cervical plexus were studied in nineteen mammalian species.

2. Communications between the facial nerve and the ophthalmic and maxillary divisions of the trigeminal and the cervical plexus were inconstant in this series.

3. Communications between the facial and derivatives of the mandibular division of the trigeminal were found invariably. In all species studied there was communication with the auriculotemporal nerve ; findings related to the buccal and mental branches and to the nerve to mylohyoid were variable.

ACKNOWLEDGMENTS

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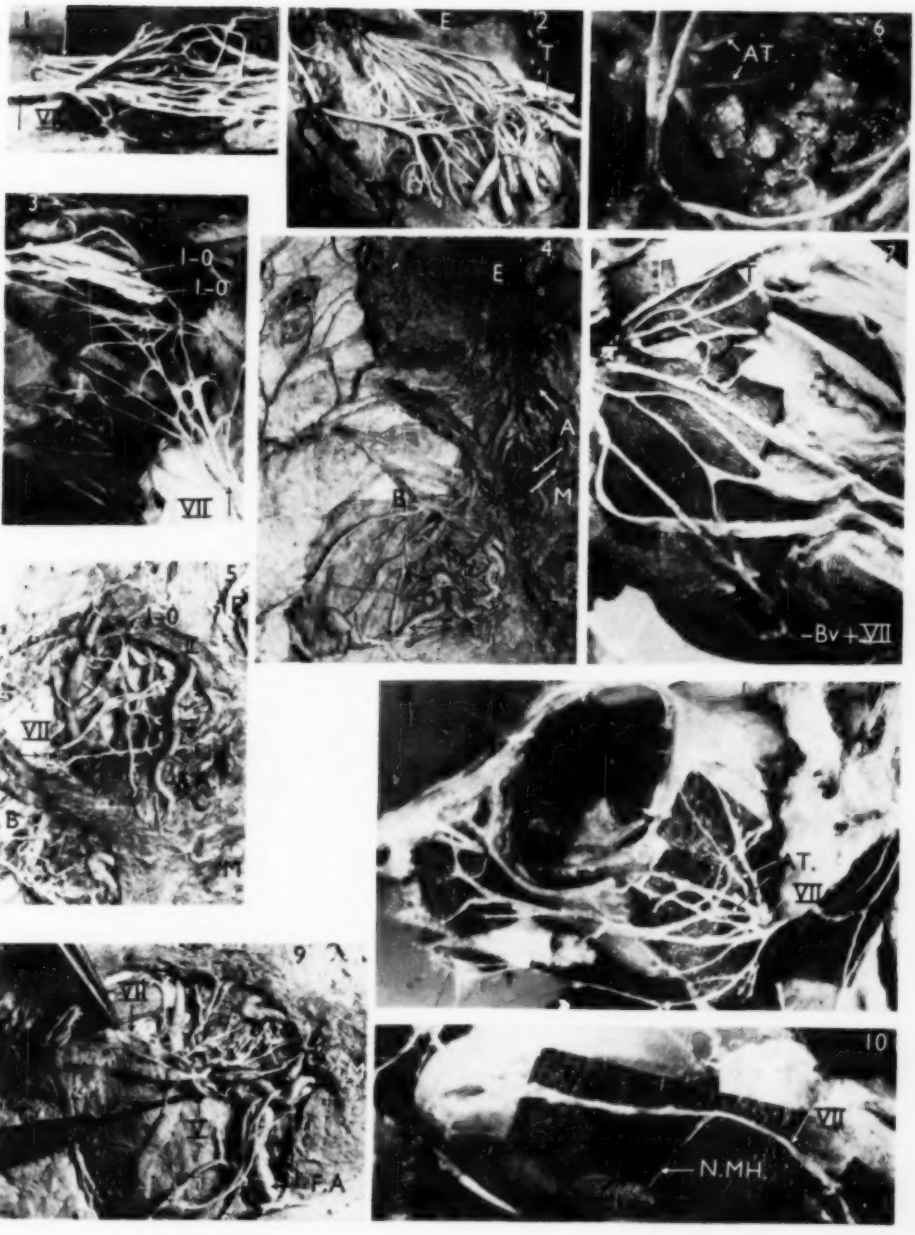

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EXPLANATION OF PLATE

1–0, Infraorbital nerve ; AT, auriculo-temporal nerve ; VII, facial nerve ; F–A, facial artery.

Fig. 1.—Right side of snout of *Tupaia tana* showing communications between the infra-orbital branches of the trigeminal and the facial nerve.

„ 2.—Right side of snout of *Phoca*, showing communications between the infraorbital nerve and the facial. T = theca of vibrissa.

„ 3.—Right side of face of *Papio hamadryas* showing communications between the infra-orbital nerves and the facial.

„ 4 & 5.—Right side of face in two human subjects, E = upper eyelid. M = angle of mouth, A = infraorbital plexus, B = buccal plexus between trigeminal and facial nerves.

„ 6.—Right side of face in human subject, showing simple communications between the auriculo-temporal and the upper division of the facial nerve.

„ 7.—Right side of face of *Tupaia tana* showing plexiform communications between the auriculo-temporal and the facial nerves. B V and VII = communication between buccal branches of the trigeminal and facial nerve.

„ 8.—Left side of face of *Tarsius spectrum* showing plexiform communication between the auriculo-temporal and facial nerves.

„ 9.—Right side of face of third human subject showing details of the buccal plexus between the trigeminal and facial nerves.

„ 10.—Left side of lower jaw of *Tarsius spectrum* showing communication from the nerve to mylohoid and the facial nerve.

ZOOPLANKTON OF THE RIVER SOKOTO
THE FRESHWATER MEDUSA *LIMNOCNIDA*

BY

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[Accepted 8th March 1960]

(With 3 figures in the text)

The freshwater medusa *Limnocnida victoriae* was found from December 1956 to April 1957 in a pool which becomes separated from the main channel of the River Sokoto during the dry season. The medusae are described and the importance of the number and size of statocysts as a systematic character within the genus is discussed. A map showing the distribution of *Limnocnida* in Africa is given.

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INTRODUCTION

The present paper is concerned with a medusa which appeared in the pool Fesafari which becomes separated from the main channel of the river during the dry season. A general account of the hydrology of this North Nigerian river and of the main fluctuations in the total plankton is given by Holden & Green (1960).

The history of the discovery of *Limnocnida* has been told many times (e.g. Günther, 1893 ; Moore, 1899 ; Brown, 1908 ; Schouteden, 1939 ; Kramp, 1954) and recently a detailed monograph of the genus has been given by Bouillon (1956–7). The last author considers that there are three African species in the genus, while other authors (Leloup, 1951 ; Kramp, 1954) have been inclined to the view that all the African forms belong to one species. The specimens from Fesafari have been examined to see if they support either of these opposing views.

TEMPORAL OCCURRENCE AND SIZE

Although the area was visited and plankton samples were taken by Mr Holden at intervals throughout the various years there were no signs of the medusa in 1954, 1955 or 1956. The first large specimens were found in February 1957, but a careful search of plankton samples taken in January of that year and December 1956 revealed the presence of very small medusae. The numbers of medusae found in a standard plankton tow over a distance of

300 metres using a net with a mouth diameter of 30·5 cm. were as follows : December, 2 ; January, 7 ; February, 35 ; March, 21 ; April, 7. There was a clear peak of abundance in February, followed by a gradual decline. Fig. 1 shows that production of small medusae persisted into March. No small specimens were found in April, and by May all the medusae had disappeared.

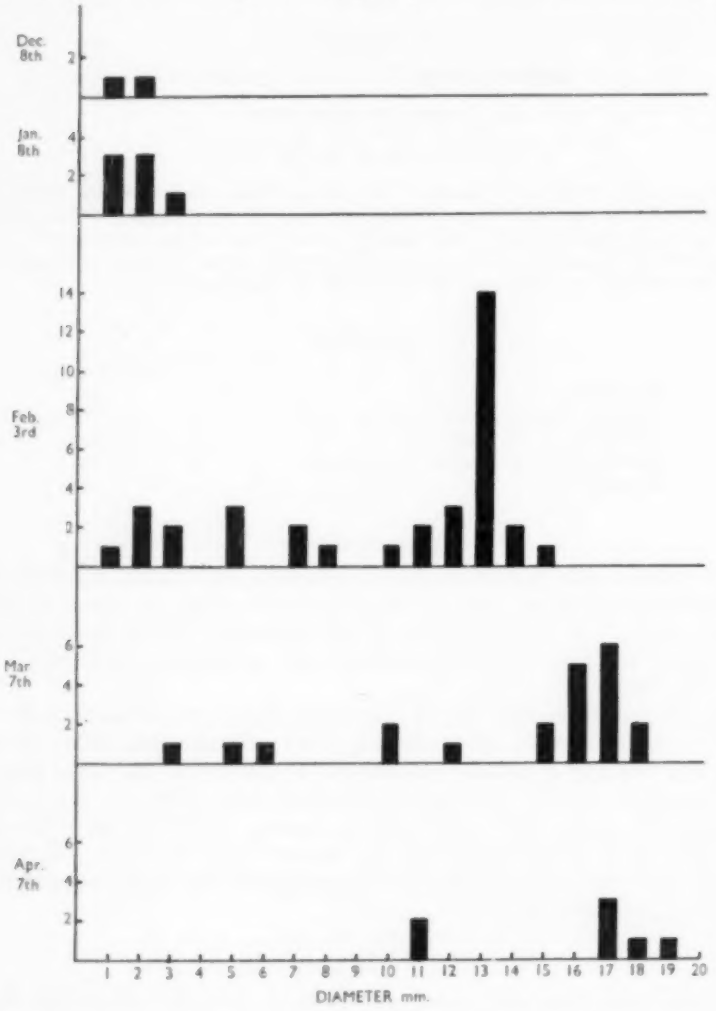

Fig. 1.—Diagram showing the frequencies of size groups of medusae of *Limnocnida* during the period of occurrence in the Sokoto river system.

Some of the larger specimens collected in February had well-developed gonads and so were presumably capable of breeding. The largest specimens

from Fesafari are distinctly smaller than those recorded from elsewhere. Diameters up to 25 mm. have been recorded from other parts of Africa, but the largest specimens from Fesafari only reach a diameter of 19 mm. There were no signs of asexual reproduction by budding around the edge of the manubrium, as is found in specimens from Lake Tanganyika.

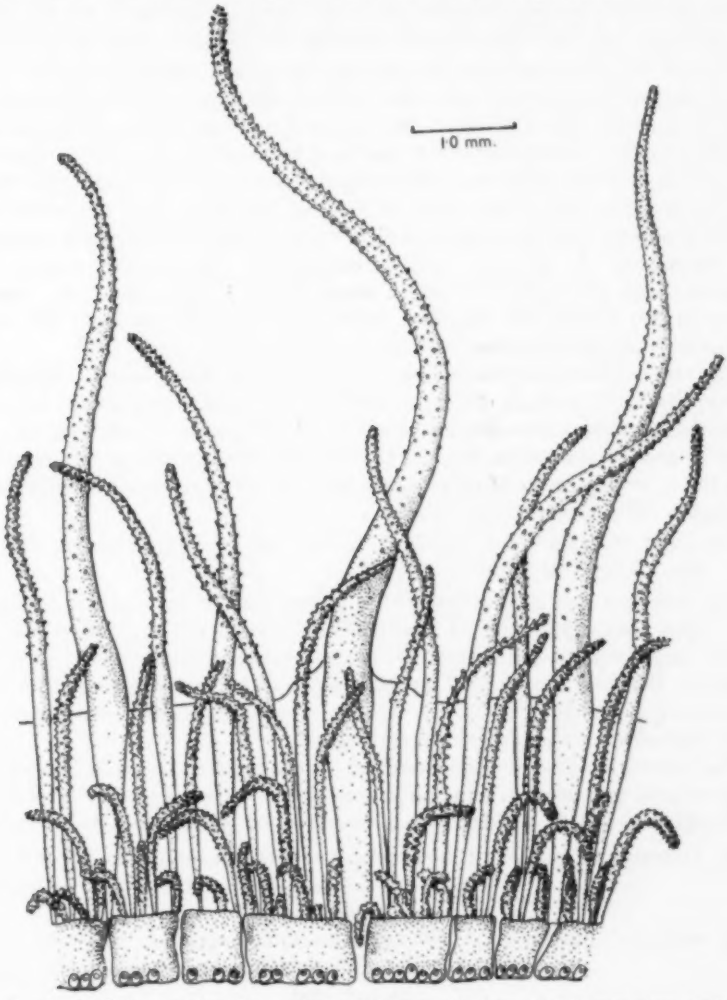

Fig. 2.—Part of the margin of a medusa of *Limnocnida* from the Sokoto river system. (Scale 1·0 mm).

The observed occurrence in Fesafari contrasts with that known in other areas. Medusae have been found in all months in Lake Tanganyika (see table on p. 267 in Bouillon, 1956–7), and in Lake Mohasi sexually reproducing individuals are found from mid-April to September (Bouillon, 1954).

DESCRIPTION OF THE MEDUSA

The characters which have been used to separate species of *Limnocnida* have been mainly the number and size of the tentacles and the marginal statocysts which lie in a row at the inner margin of the ring of nematocysts.

In the specimens from Fesafari there are about 400 tentacles on an individual with a diameter of 15 mm. The tentacles are arranged in a fairly definite series (Fig. 2). The largest tentacles are about 1 cm. in length. The number of tentacles increases as the animal grows. Bouillon (1955) notes that when freshly budded from the hydroid the medusa has a diameter of 0·4 mm. and has eight tentacles. The smallest specimen found in the plankton from Fesafari had a diameter of 0·6 mm. and had eight tentacles. A specimen with a diameter of 1·0 mm. had eight tentacles and the rudiments of eight more, while a specimen with a diameter of 1·4 mm. had eight long tentacles, eight shorter tentacles and the rudiments of 16 more ; none of these small specimens had statocysts. A specimen with a diameter of 2·5 mm. had a total of 32 tentacles, with the rudiments of 32 more, and 16 statocysts were present. Edney (1939) noted that the first eight statocysts appeared in Rhodesian specimens when the diameter was about 2·0 mm.

The size of the statocysts has been thought to be of systematic importance. Most authors give a single diameter, as if the statocysts were always spherical, but in the specimens from Fesafari most of the statocysts are egg shaped. The range of size of statocysts from a 13 mm. diameter specimen can be judged from the following series of measurements made on 10 successive neighbouring statocysts (measurements in μ) :

130×104, 91×65, 130×117, 78×78, 104×91, 65×65, 130×130, 104×91, 95×78, and 104×91.

The average size is thus somewhat larger than that found in specimens from Lake Tanganyika, where Bouillon (1956–7) found an average diameter of 75 μ, and Arnold & Boulenger (1915) give a range of diameters from 70–90 μ. However, Bouillon has pointed out that some statocysts in Tanganyika specimens reach a diameter of 142 μ. It would seem that not much importance can be attached to the size of the statocysts.

The number of statocysts in relation to the number of tentacles might be of systematic importance. In specimens from Fesafari the ratio is about 0·6.

Bouillon (1956–7) divides the African species of *Limnocnida* as follows :

L. tanganyicae Günther : 300 tentacles, with maximum length of 2·0 cm., ratio of statocysts to tentacles 0·80, medusae produce buds.

L. victoriae Günther : 400 tentacles, with maximum length of 1·6 cm., ratio of statocysts to tentacles 0·93, medusae do not bud.

L. congoensis Bouillon : 800 tentacles, with maximum length of 1·2 cm., ratio of statocysts to tentacles 0·48, medusae do not bud.

On the basis of the number of tentacles and the lack of budding the medusae from Fesafari clearly belong to *L. victoriae*. The tentacles do not, however,

reach a length greater than 1·0 cm., though this may be due to shrinkage on fixation. The ratio of the number of statocysts to the number of tentacles is distinctly low. This may be due to some extent to the generally small size of the Sokoto specimens. Browne (1908), in his study of two specimens from the Niger delta, noted that the larger specimen (18 mm. diam.) had an almost continuous row of statocysts all touching each other, while the smaller specimen (11 mm. diam.) had a much less crowded row with small gaps.

Fig. 3.—The distribution of *Limnocnida* in Africa. Dots indicate localities where medusae have been collected. Crosses indicate places where medusae have been observed but not collected.

The specimens from Fesafari do not invalidate the specific categories set up by Bouillon, but they do indicate that the ratio of statocysts to tentacles is

not a very reliable character, and certainly not one of sufficient accuracy to warrant quoting to the second decimal place.

DISTRIBUTION OF *LIMNOCNIDA* IN AFRICA

On Bouillon's map (1956–7, p. 469) only a single record from West Africa is shown ; this is the record by Daget (1950) from the upper reaches of the Niger. In fact there are at least three other authentic records of *Limnocnida* from West Africa. Browne (1908) gave a detailed description of two specimens collected by J. S. Budgett from the Niger delta, and Dekeyser (1955) gives details of the other occurrences. A revised map of the distribution of *Limnocnida* in Africa is given in Fig. 3. Of the three species recognized by Bouillon (1956–7), *L. tanganyicae* is found only in Lake Tanganyika, *L. congoensis* is found in the River Congo, and *L. victoriae* occurs in all the other localities.

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OBSERVATIONS ON THE BEHAVIOUR OF SOME ORIBATID MITES IN EXPERIMENTALLY-CONTROLLED TEMPERATURE GRADIENTS

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[Accepted 12th April 1960]

A description is given of the behaviour of oribatid mites from West Africa and North America in temperature gradients. The results of the experiments may be summarized as follows :—

(i) West African species had a tolerance zone of 18° C.–36° C. compared with 16° C.–28° C. in North American species.

(ii) West African species had an upper critical temperature and an upper lethal temperature of 37° C. and 38° C.–40° C. respectively, compared with 30° C. and 30° C.–32° C. respectively in North American species.

(iii) Most West African species had a preference for conditions in the 24° C.–31° C. range, compared with 21° C.–26° C. in North American species.

The differences between the two groups depended very largely on the temperature conditions to which the mites had been exposed before the experiments. Evidence of an avoiding reaction by many mites to extreme temperature conditions in the gradient provides a partial explanation for the seasonal change in the distribution of mites in the soil profile.

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INTRODUCTION

Within the past twenty-five years ecological investigations into the distribution, population dynamics, and habits, of soil-inhabiting Oribatei have revealed the importance of this group in the litter decomposition process. It is generally recognized that microclimatic factors can influence, to some extent at least, the distribution and changes in population size of soil Oribatei (van der Drift 1951, Bellinger 1954, Kühnelt 1955). Although soil moisture is regarded as one of the most important factors in this respect (Riha 1951, Kühnelt 1955, Murphy 1955), van der Drift (1951) has shown that there is some correlation between changes in population density of certain Oribatei,

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notably *Nothrus silvestris* (juveniles), *Belba minutissima* (adults), and *Oribotritia loricata* (adults), and changes in soil temperature. The responses of oribatid mites to various temperature conditions have been deduced from field observations on changing patterns of distribution, in the majority of cases. Apart from the studies of Handschin (1929) and Dalenius & Wilson (1958), there have been very few attempts to investigate these responses using controlled experimental conditions.

The observations and experiments described below were designed to record the behaviour of a number of species of Oribatei in a temperature gradient and under controlled experimental conditions. The study was started at the University of Michigan, U.S.A., using mites from a Hemlock-Yellow Birch forest floor, and continued at the University College of Ghana, using mites from thicket and grassland soils in Southern Ghana.

MATERIALS AND METHODS

The temperature gradient was set up in a glass tube 90 cm. long with an internal diameter of 1·5 cm. Holes were blown in the wall at 15 cm. intervals along its length to permit the introduction of a thermometer bulb. Four thermometers were sealed in place with plasticine, and a fifth was inserted in the glass tube from one end (the cold end). A thin strip of white paper was placed inside the tube to provide a surface for the mites to walk on, and also to allow the observer to see the mites clearly. This glass tube was then placed inside a longer brass tube from which a longitudinal section of the wall had been removed. One end of the brass tube was enclosed in ice ; a heating coil of Nichrome wire was wound around the other. This heating coil was connected through a transformer to the mains supply. A variable resistance was included in the circuit so that the temperature of the coil could be controlled at 40° C. The brass tube was lagged with cotton wool to prevent much heat exchange with the surrounding air. Conditions of uniform illumination were maintained along the length of the tube during the experiments. A range of temperature conditions from 4° to 50° C. could be established in the glass tube using this apparatus, although in practice the temperatures at the five thermometer positions were : (1) 15° C. (±2° C.) ; (2) 20° C. (±2° C.) ; (3) 25° C. (±1° C.) ; (4) 30° C. (±1° C.) ; (5) 35° C. (±2° C.). The temperature in the immediate vicinity of the heating coil was 40 ° C.

The duration of each experiment was approximately three hours, and during this time a continuous flow of air was pumped along the glass tube from the hot end to the cold by an aspirator system, at a rate of 60 c.c./min. This rate of flow did not affect the established gradient. The relative humidity of the air passing into the gradient in the Ghanaian experiments was 70 per cent (dew-point = 22° C.), and in the North American experiments 65 per cent (dew-point = 18° C.). Variations of 3–5 per cent in the relative humidity values occurred over the whole period of the experiments. Air dried over calcium chloride (relative humidity = 40 per cent ; dew-point = 13° C.) was passed through the glass tube in three experiments designed to detect any departures from the normal pattern of behaviour, using conditions of lower relative humidity. These experiments involved five individuals of the

following species : *Pergalumna longisetosa* Bal., *Scheloribates leleupi* Bal. (thicket form), and *Phthiracarus* sp. 1. A comparison between these results and another series using the same individuals under the more usual conditions described above revealed no major differences in behaviour and final distributions of the mites.

Preliminary observations on oribatid mites in cultures and in temperature gradients showed that these mites very rarely remain stationary under tolerable conditions, unless they are feeding. Activity almost always consists of an exploration of the immediate surroundings, the tactile hairs on the first pair of legs and the palps being used for this purpose. Many oribatid mites will become immobile when suddenly disturbed or when subjected to extreme temperature conditions. In these cases the mouth parts are retracted and the legs drawn close to the sides of the body, so that the animals rest on their ventral surfaces. On the other hand, many mites will move away from extreme temperature conditions, and this avoiding reaction is characterized by a relatively rapid rate of movement directly away from the unfavourable conditions. This avoiding movement can be distinguished easily from the exploratory activity in that the rate of progress is increased, lateral exploratory movements do not occur, and small objects in the path, such as detritus particles which may serve as food, are ignored.

Observations on the reactions described above are the bases of this study of behaviour. Mites were introduced into the temperature gradient through the holes in the glass tube at the thermometer positions. Each mite was examined with a binocular microscope immediately after its insertion into the tube, to ensure that it was moving in a normal manner at this stage. Twenty experiments were carried out on single individuals of each of the North American species, a total of five individuals of each species being introduced into the gradient at each of four thermometer positions. Observations on the position of the mite, its direction of movement, and the type of movement, were made at 2-minute intervals. Later (in the experiments carried out in Ghana) groups of individuals of the same species were placed in the gradient in a regular manner, and only two experiments were carried out on each species. The time interval between observations was extended to 15 minutes, except in cases of mites on or near the borderlines between two temperature zones. This time interval prevented the observer suffering undue strain over an extended period and was sufficiently small to permit a fairly accurate assessment of changes of position to be made. Observations on *P. longisetosa* were made at 2-minute intervals, for this was a large and active mite.

The observations are expressed in terms of the final positions of the mites and also in the amount of time spent by individuals in each of the temperature zones. Two main difficulties were encountered in the experiments. The first of these was that mites placed directly into extreme temperature conditions frequently became immobile, and remained in this state throughout the experiment. The time spent in this condition did not reflect a preference on the part of the mites, and account was taken of this fact in the analysis of the results. Secondly, the change in temperature along the gradient was not

always strictly linear ; the temperature difference between the middle thermometers frequently was slightly less than that between the middle and end thermometers. It was difficult in some cases to determine the temperature in certain parts of the gradient, particularly at points equidistant between two thermometers, for this reason. Records of the amount of time spent by mites in a particular temperature zone were only made if the temperature was known or could be inferred with some degree of certainty.

All mites were preconditioned for a 12-hour period before the experiments. The preconditioning temperatures in the West African and North American experiments were 30° C. and 23° C. respectively. These corresponded to normal litter temperatures at mid-day during the hottest part of the year, in the respective localities, but did not represent the maximum litter temperatures in these localities.

The species of West African Oribatei are new species and are presently being described by Balogh (1958, 1959). Dr Balogh has very kindly identified the species for me.

DEFINITIONS

The terms used in this description are not new, but definitions are included in this section to avoid confusion over their interpretation.

The tolerance zone of a species is that range of temperature conditions within which more than 50 per cent of the individuals show active movements.

The preference zone of a species is that range of temperature conditions most suitable for the normal exploratory activities of the mites. More than 50 per cent show no avoiding reaction within this zone, nor do they remain completely immobile with mouth parts and legs withdrawn for long periods.

The lethal temperature is here defined as that temperature condition nearest to the upper or lower limit of the tolerance zone causing mortality of more than 50 per cent after an exposure time of 30 minutes. Upper and lower lethal temperatures, due to heating and cooling respectively, are included in this definition.

Mites may become immobile in temperature conditions outside the upper and lower limits of the tolerance zone. Conditions of heat and cold immobility are recognized. The studies of Dalenius & Wilson (1958) have drawn attention to the fact that cold rigor is preceded by a period of cold immobility. These workers noted that it was difficult to distinguish between these two conditions. Experiments carried out during the present work showed that the same is true for heat immobility and rigor, in many cases, although in some instances different stages in the immobile condition were recognized. These were particularly marked in species of the family Galumnidae. In *Galumnella areolata* Bal. (thicket form) heat immobility was preceded by violent aimless movements which soon subsided as the legs were withdrawn beneath the pteromorphae. During the initial period of immobility leg movements continued, although the legs were partly withdrawn, and the pteromorphae moved up and down in a beating motion. At this stage the mites would recover completely if placed in temperature conditions within their preference zone. The second stage of heat immobility was marked by cessation of leg

movements and the complete withdrawal of the legs beneath the pteromorphae. The pteromorphae continued to move up and down at this stage. Recovery from this condition was usually incomplete for although the mites were able to walk, their progress was slow and not completely co-ordinated. The final stage in the immobile condition was characterized by a faint beat of the pteromorphae, but this became irregular and finally ceased. During this period heat rigor set in and was followed by death. Mites in this final stage of immobility and rigor did not recover.

The temperature condition producing the initial stage of immobility is referred to herein as the critical limit. Upper and lower critical limits are recognized ; these fall just outside the upper and lower limits of the tolerance zone.

OBSERVATIONS AND RESULTS

Table 1 shows the distribution of mites along the temperature gradient at the end of the experiments. Active and torpid individuals are included in the Table ; an asterisk (*) denotes that all or some of the mites in a particular group were recovered in a torpid state at the end of the experiments. The results for each species represent sum totals of mites used in the series of experiments.

TABLE 1

The final distribution of mites, represented by sum totals, in the various temperature zones. (An asterisk (*) denotes that the number includes torpid individuals.)

Species	Number of mites used	Final number in each Zone				
		15° C.–20° C.	20° C.–25° C.	25° C.–30° C.	30° C.–35° C.	35° C.–40° C.
(West African)						
Galumnella areolata Bal.	17	3	2	8	2	2
G. areolata (grassland form)	15	2	8	3	2	0
Pergalumna frater Bal.	17	4*	3	7	1	2*
Pergalumna longisetosa Bal.	28	12	5	7	4	0
Carabodes sp. 1 (n. sp.)	13	2*	1	2*	8*	0
Peloribates sp. 1 (n. sp.)	11	0	0	6*	1	4*
Scheloribates leleupi Bal.	17	1	4	11	1	0
S. leleupi (grassland form)	11	0	2	9	0	0
Phthiracarus sp. 1 (n. sp.)	17	2*	2	7	2	4*
(North American)						
Tectocepheus velatus (Koch)	20	0	11	4	1*	4*
Gymnodamaeus bicostatus (Koch)	20	4	3	5	4*	4*
Fuscozetes fuscipes (Koch)	20	3	4	5	4*	4*
Phthiracarus borealis (Trgdh.)	20	4	5	5	2*	4*
Oppia neerlandica (Oudms.)	20	0	9	4	3*	4*
Peloribates sp. 2 (n. sp.)	20	2	6	4	4*	4*
Achipteria coleoptrata L.	20	3	7	2	4*	4*

The final distribution of active and torpid mites in the gradient reflects, to some extent, the limits of the tolerance zone. Accumulations of mites showing normal exploratory activity, in certain parts of the gradient, may also be an indication of temperature conditions suitable for this type of activity, but

although the final distribution is determined by previous activity or inactivity of the mites, it does not measure this activity and has only a very limited use in determining tolerance and preference zones, for this reason.

TABLE 2

The amount of time spent by mites, represented by sum totals, in the various temperature zones during the course of the experiments.

Species	Number of mites used	Total time spent in each Zone (in mins.) 15° C.–20° C.	20° C.–25° C.	25° C.–30° C.	30° C.–35° C.	35° C.–40° C.
(West African)						
Galumnella areolata Bal.	15	135	300	510	315	120
G. areolata (grassland form)	15	210	426	500	420	34
Pergalumna frater Bal.	11	150	100	540	20	20
Pergalumna longisetosa Bal.	14	798	140	434	42	14
Scheloribates leleupi Bal.	12	84	360	624	204	24
S. leleupi (grassland form)	10	120	210	540	210	0
Phthiracarus sp 1 (n. sp.)	12	0	144	912	180	0
(North American)						
Tectocepheus velatus (Koch)	12	0	760	86	0	0
Gymnodameus bicostatus (Koch)	12	275	356	315	0	0
Fuscozetes fuscipes (Koch)	12	150	308	423	0	0
Phthiracarus borealis (Trgdh.)	12	327	483	405	0	0
Oppia neerlandica (Oudms.)	12	20	912	322	0	0
Peloribates sp. 2 (n. sp.)	12	120	525	342	0	0
Achipteria coleoptrata L.	12	35	540	93	0	0

The amount of time spent by the mites in each temperature zone is a much more reliable criterion of activity. Table 2 shows the results of this experimental method, represented by sum totals of the amount of time spent in each zone by the mites. The time spent in various zones by mites in a torpid state is not included in the Table in order to give a more accurate impression of the preference zones. Torpid or completely immobile individuals of the West African species of *Carabodes* sp. 1 and *Peloribates* sp. 1 constituted such a large proportion of the mites used that the results for these species were inconclusive and have been omitted from the Table. The following conclusions may be drawn from the results given in Tables 1 and 2 :—

West African species

Individuals of most species were active within a broad tolerance zone extending from 18° to 36° C., although many mites moved down the gradient from temperature conditions in the upper part of the 30° C.–35° C. zone. The avoiding reaction was shown to a very marked degree by mites of all species to temperature conditions between 35 and 37° C., although the thicket and grassland forms of *G. areolata* showed a slightly greater degree of tolerance to temperature conditions in the 35 to 38° C. range. The upper and lower critical limits for most species were 37° C. and 17° C. respectively ; exceptions to this being the thicket and grassland forms of *G. areolata* with an upper critical limit of 39° C.

Preference zones were rather more variable than tolerance zones. The amount of time spent by individuals of *Phthiracarus* sp. 1 and the thicket and grassland forms of *S. leleupi* in the 25° C.–30° C. zone was substantially greater than that in any other zone (Table 2). The final distribution in the gradient of mites of these three groups also reflects this preference (Table 1). The preference zone for the remaining West African species appears to extend over a much wider temperature range, but in fact this zone is not as broad as the results given in Table 2 suggest. Normal exploratory activities continued just outside the upper and lower limits of the 25° C.–30° C. zone in the thicket and grassland forms of *G. areolata*, and the preference zone could be limited to 24° C.–31° C. *Pergalumna frater* and *P. longisetosa* preferred temperature conditions within the 18° C.–26° C. zone, the former species preferring conditions in the upper part, the latter in the lower part, of this zone. It was not possible to define preference zones in the cases of *Carabodes sp.* 1 and *Peloribates sp.* 1. These mites were usually inactive in the gradient and showed little or no avoiding movement in the high and low temperature zones. The numbers of individuals used were rather small in both cases ; larger samples may have revealed more definite preferences, particularly in the case of *Peloribates sp.* 1, for these mites were quite active in cultures at 30° C. A feature of both these species was the ability to survive conditions of high temperature, for five individuals of each recovered completely after exposure to temperatures of 40° C.–41° C. for a 2-hour period.

The upper lethal temperature for the thicket species, with the exception of *G. areolata*, *Carabodes sp.* 1, and *Peloribates sp.* 1, was between 38 and 40° C. These three exceptions, together with the grassland form of *G. areolata*, had an upper lethal temperature of 42° C. The lower lethal temperature was not investigated fully in these studies, for a very large majority of the mites subjected to temperature conditions below the lower critical limit recovered, although the recovery was sometimes incomplete. In general there was a much better resistance, in terms of numbers surviving, to conditions below the lower critical limit, than there was to conditions above the upper critical limit. This was clearly demonstrated by the thicket form of *G. areolata* and by *P. longisetosa*. Ten mites of each of these species were exposed to temperature conditions within the range 4° C.–10° C. for 1 hour, from which all recovered completely.

North American species

The tolerance zone was generally narrower than that of the West African species, occupying a range from 16 to 28° C. *T. velatus* was active only within a zone extending from 20 to 26° C. Most species avoided temperature conditions outside or near to the limits of the tolerance zone ; this avoiding reaction was strongly developed in *T. velatus*. All of the mites placed in the 35° C.–40° C. zone became immobile almost immediately, as did the majority of those placed in the 30° C.–35° C. zone. Those escaping from the latter zone moved down the gradient rapidly, and the amount of time spent moving from this zone to the lower ones was insignificant and has not been recorded in Table 2. No avoiding reaction to high or low temperature conditions was shown by

individuals of *G. bicostatus* and *F. fuscipes*, although heat immobility occurred at 30° C. The upper and lower critical limits for most species were 30 °C. and 15° C. respectively ; in the case of *T. velatus* they were 27° C. and 19° C. respectively.

The preference zones for the majority of species lay within a range of temperature conditions extending from 21 to 26° C. (Table 2), although *G. bicostatus*, *F. fuscipes*, and *P. borealis* could not be restricted to such a narrow zone. The results for these three species are inconclusive, as far as preference zones are concerned. *A. coleoptrata* and *T. velatus* showed a preference for conditions in the 21° C.–24° C. range.

The upper lethal temperature for all the North American species studied lay within the 30° C.–32° C. zone. Some species could withstand temperature conditions in this zone longer than others. Twenty individuals of *O. neerlandica*, exposed to a temperature of 30° C. for 45 min. developed heat immobility from which eighteen recovered completely. The upper lethal temperature for this species was 32° C. *T. velatus* had a prolonged period of heat immobility within the range 27° C.–31° C., and seventeen out of twenty survived after exposure at 32° C. for a 10 min. period. *P. borealis* also appeared to have a high degree of tolerance to temperature conditions in the 29° C.–31° C. range. As in the West African species, the lower lethal temperature was not discovered, for all mites recovered from exposure to temperature conditions below the lower critical limit in the 4 to 15° C. range.

The preconditioning temperature

The behaviour of animals in a temperature gradient may be affected by the temperature conditions to which they have been exposed before the experiment. Chapman (1955) noted that the preference zone of fifth-instar hoppers of *Locusta migratoria migratorioides* (R. & F.) was a function of the preconditioning temperature.

The effect of preconditioning on the behaviour of fifteen individuals of the grassland form of *G. areolata* was investigated by placing these mites in plaster of Paris culture cells (Edwards 1955), maintained at a temperature of 23° C., before placing them in the temperature gradient. This pre-treatment had no significant effect when carried out for a two-hour period ; the pattern of behaviour of the mites in the gradient was very similar to that of the mites preconditioned for 12 hours at 30° C. Differences were observed after a four-hour preconditioning period ; the results of this experiment are shown in Table 3. The results of observations on fifteen individuals of this species, preconditioned for 12 hours at 30° C. are repeated in this Table for comparison. Preconditioning at 23° C. for four hours had a marked effect on the tolerance zone, which was reduced to a temperature range between 16 and 30° C., and on the upper critical limit, which was lowered to 32° C. The preference zone was not clearly defined although there was some accumulation of individuals below 25° C. The upper lethal temperature (42° C.) was not affected. The depression of the upper critical limit was accompanied by an extension of the period of heat immobility.

TABLE 3

The effect of two different preconditioning treatments on the behaviour of the grassland form of *Galumnella areolata* Bal. (*a*) The final distribution in the temperature zones. (An asterisk (*) denotes that the number includes torpid individuals.) (*b*) The amount of time spent in the various temperature zones.

(*a*)

Pre-Treatment	Number of mites used	Final number in each Zone 15° C.–20° C.	20° C.–25° C.	25° C.–30° C.	30° C.–35° C.	35° C.–40° C.
Preconditioned at 30° C. for 12 hours	15	2	8	3	2	0
Preconditioned at 23° C. for 4 hours	15	4	2	3	4*	2*

(*b*)

Pre-Treatment	Number of Mites used	Total time spent in each Zone (in mins.) 15° C.–20° C.	20° C.–25° C.	25° C.–30° C.	30° C.–35° C.	35° C.–40° C.
Preconditioned at 30° C. for 12 hours	15	210	426	500	420	34
Preconditioned at 23° C. for 4 hours	15	390	345	546	0	0

The ability of mites to react fairly rapidly to preconditioning temperatures was shown particularly well by the North American species. *Peloribates sp.* 2 normally went into heat immobility at 29° C. when preconditioned at 23° C. for 12 hours. Five mites of this species remained active at 30° C. after being preconditioned at 28° C. for a 40-minute period. Activity persisted up to 32° C. if the preconditioning period was extended to 80 minutes but this was the upper limit. The upper limit of the tolerance range of five individuals of *A. coleoptrata* was extended to 31° C. after preconditioning at 28° C. for 70 minutes. Although individuals of *T. velatus* preconditioned at 23° C. for 12 hours appeared to have good powers of heat resistance to temperature conditions in the 29° C.–32° C. range, preconditioning at 27° C. for long periods did not produce activity under these conditions. The upper limit of the tolerance zone of five individuals of *P. borealis* was extended to 30° C. after preconditioning at 28° C. for a period of 30 minutes.

DISCUSSION

The major differences between the behaviour patterns of West African and North American species depend very largely on the preconditioning temperatures which, in themselves, represent temperature conditions occurring at certain times at the respective localities. Some aspects of behaviour, such as those reflected in the limits of the tolerance zone and in the critical limits, are therefore conditioned, rather than innate, responses, which are adapted to the natural conditions found in the respective sampling localities.

Field studies on the distribution and dynamics of North American species in the forest floor were carried out concurrently with part of the present work (Wallwork 1959). These showed that the number of adult mites decreased

in litter and increased in humus during the warmest (July–August) and coldest (November–February) periods of the year, the change in litter populations during the summer being slight compared with the change in winter. Movement down from litter to humus by adults of several species appeared to be a factor in these changes, although they could not be interpreted solely in these terms. This movement may have been a response to changing temperature conditions in the litter ; moisture values did not change appreciably in litter and humus during these periods. The maximum litter temperature during the summer (25° C.) approached the upper limit of the tolerance zone of some species (e.g. *T. velatus*), and may have produced an avoiding response which would be sufficient, even on a small scale, to account for the slight decrease in numbers in litter in summer. This maximum was rather lower than the upper limit of the tolerance zone of most species however, and was not a limiting factor in these cases. There was a much greater change in winter when the litter temperature dropped to 0° C. There was also a much greater decrease in the litter population, although the humus population continued to rise steadily. The temperature condition corresponding to the lower limit of the tolerance zone of most species occurred first in litter, and may have caused a downward movement of mites. The decrease in number of adults of *O. neerlandica* in litter at the onset of winter corresponded closely to the increase in number in humus. Movement from litter to humus has been suggested as an explanation for these changes (Wallwork 1959). Observations on these mites in the temperature gradient support this view, for a strong avoiding reaction to conditions in the 15° C.–20° C. zone was shown (Tables 1 and 2). Many of the North American and West African species tested in the gradient showed a much better ability to withstand relatively cold conditions than relatively warm ones. This was also demonstrated by the fact that many mites were extracted alive from frozen soil samples in North America.

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NOTES ON THE BREEDING OF THE DOMESTICATED GREY GUPPY *LEBISTES RETICULATUS* (PETERS)

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(With 3 figures in the text)

The broods from guppies *Lebistes reticulatus* are usually small owing to cannibalism by the parent and other fish before the swim-bladders of the fry are inflated. When cannibalism is eliminated, by confining each female in a maternity cage, the number of fry in the brood from domesticated grey guppies is a linear function of the total length of the female.

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INTRODUCTION

The guppy—*Lebistes reticulatus* (Peters)—a viviparous cyprinodont, has been used by many workers in genetical and other studies. In these studies there are only a few incidental references to the sizes of the broods. Winge (1922) stated that there are generally ten to fifty young. Rosenthal & Rosenthal (1950) wrote, " fertility appears normal with broods ranging from two to thirty-six depending on the size and age of the female ". From other papers—Goodrich *et al.* (1944) and Hildemann & Wagner (1954)—it is possible to calculate the average size of the broods. It is apparent from the small broods recorded in these and other papers that the cultural methods employed in keeping the fish resulted in losses.

This paper is concerned with the mortality of grey guppies just after birth and with the size of the brood in relation to the size of the female fish.

THE TYPICAL CULTURAL METHOD

Domesticated guppies are bred and kept as pets by aquarists in many countries. The fish are housed in tanks, usually with glass sides, containing one or more gallons of water and planted with *Sagittaria*, *Vallisneria* and other aquatic plants.

It is well known that young guppies are eaten by the adult fish but aquarists maintain that in " heavily planted " tanks the young are able to escape and few, if any, are eaten.

The young fish are fed on various artificial foods occasionally supplemented with live *Daphnia*, *Cyclops* or other small crustaceans. The growth of the fish is comparatively uniform for the first few days but afterwards great variations may occur, especially if the tank is overcrowded.

INFLATION OF THE SWIM-BLADDER AND CANNIBALISM

Rosenthal (1951) described " the birth process of the guppy " but although he referred to the young being expelled from the female he did not describe the subsequent behaviour of the fry.

By placing a pregnant female in a small glass tank and waiting until parturition occurred it was possible to observe the subsequent behaviour of the fry.

After being expelled from the female each fry fell rapidly towards the bottom of the tank indicating that its specific gravity was greater than that of the water. Usually before reaching the bottom the fry swam vigorously towards the surface of the water and, having reached it, gulped down a small bubble of air which was forced along the pneumatic duct to the swim-bladder. Inflation of the swim-bladder reduced the specific gravity of the fish to approximately that of the water and the fry was then able to maintain its position in the water with little apparent effort and swam with the axis horizontal.

In goldfish it was noted (Affleck, 1950) that some alevins initially inflated the swim-bladder with bubbles of oxygen produced by aquatic plants. Guppies have not been observed inflating the swim-bladder in this way.

Occasionally fry were unable to inflate the swim-bladder and only swam with difficulty until either the swim-bladder was eventually inflated or they were eaten by the parent.

As soon as a fry had been expelled the parent fish usually turned round and attempted to catch and devour it. When the attempt was made before the fry reached the surface of the water the fry was almost invariably caught and eaten but once the swim-bladder had been inflated the fry had a much better chance of escaping but did not always do so.

There were considerable differences in the behaviour of the parent fish. In some cases they made no attempt to eat the young fish but in others they devoured as many as possible. The reason for such differences in behaviour is not known.

In thickly planted aquaria it is usually difficult or impossible to observe the birth of guppies but on one occasion the author saw a female fish catch and eat two fry just after they had been expelled.

A CONTROLLED CULTURAL METHOD

Innes (1917) stated that some aquarists use maternity cages in which fish are confined during parturition but that they are not favoured by professional fish breeders. They consist of a cage formed from a number of rods spaced

so that the gaps between them are large enough for the fry to pass through but too small for the parent fish to do so.

The author was able to purchase two types of maternity cages. In one, which had a bottom, the fry had to re-enter the cage in order to reach the surface of the water and inflate the swim-bladder, while in the other the parent fish was able to turn round and catch fry before they fell through the bars.

Fig. 1 shows the maternity cage that was eventually constructed to prevent parent fish devouring the fry. The ends **E** (7·5 × 5 cm.) were made of moulded polythene and had sockets **S** into which fitted polystyrene tubes **T** (15 cm.

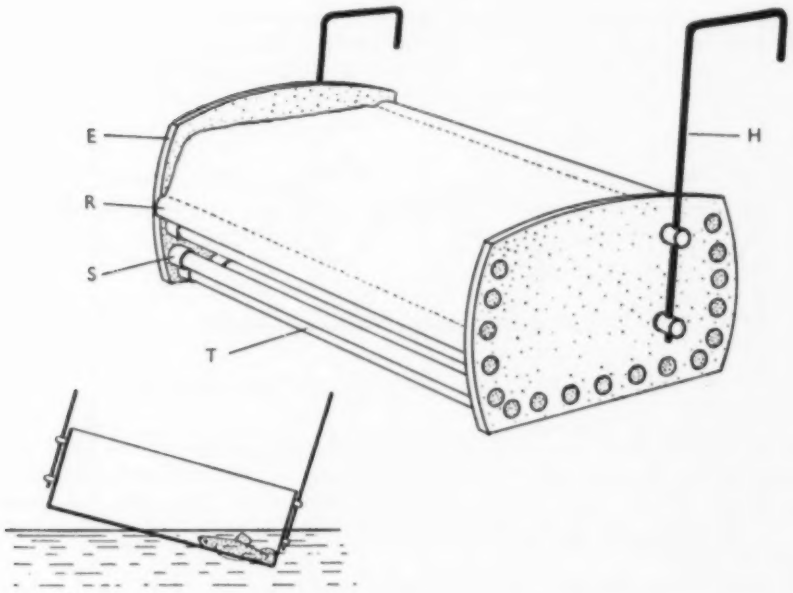

Fig. 1.—The maternity cage. Inset shows cage in use. See text for explanation of letters.

long, 5 mm. dia.). Holes (4 mm. dia.) were drilled from the exterior through the ends into the sockets. These allowed air, which would otherwise cause the cage to float, to escape from the tubes. The gaps between the tubes were 3 mm. The lid was made from nylon netting with one side threaded on to one of the top tubes. The free side of the lid was stiffened with a glass rod **R** sewn into the seam as shown. The cage was hung on the side of a tank by means of two wire hooks **H** covered with polythene tubing. One of the hooks was 2·5 cm. longer than the other so that the cage did not hang horizontally.

When the cage was in position in the tank the level of the water was adjusted so that the fish, when resting on the bars, was only just submerged. Under these conditions the fish was unable to turn round and catch the fry as they dropped through the bars.

A number of grey guppies were kept in aquaria ($40 \times 25 \times 20$ cm.) with a maximum of eight fish, including at least two males, per tank. Electric immersion heaters (40 watt), controlled by a master thermostat, maintained the temperature of the water at 24–27° C. Each tank contained a small amount of duckweed (*Lemna*) but otherwise had no plants or sand. The aquaria were situated in a small greenhouse and exposed to natural light passing through glass windows in the roof.

The fish were fed twice daily with Bemax (stabilised wheat germ) and once a week with *Daphnia* or other small crustacea.

A few days before parturition females were removed to maternity cages and kept in them until the fry were delivered. Fish ready for the cage were easily recognized because one or two days before parturition the ventral

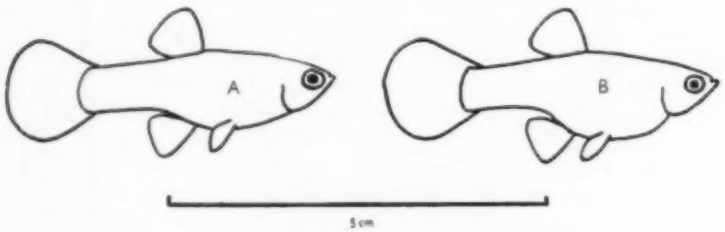

Fig. 2.—Female guppies. Specimen **B** just before parturition.

contour of the fish, posterior to the head, bulged conspicuously (Fig. 2B). When all the fry had been expelled the female was measured and returned to the tank with the males. Not more than five broods from any one female were recorded. Tanks containing the fry were emptied before the broods were counted.

Eight young females from one brood were selected at random and isolated in separate tanks. Males were placed in tanks with two of the females but the other six were not mated until each was over forty millimetres in total length. In this way first broods from large females were obtained with the other two fish acting as controls.

During the three years in which these data were recorded no fish died in a maternity cage.

THE SIZE OF BROODS

Records of the total length of each female (snout to extremity of caudal fin) at the end of parturition, and the number of fry in the brood were plotted (Fig. 3) and it was found that the size of the brood was a linear function of the length of the female. The relationship is expressed by the formula :—

$$\mathbf{N}=5{\cdot}2\,\mathbf{L}-155\pm(0{\cdot}7\,\mathbf{L}-14)$$

when **N**=number of fry in the brood ;

L=total length of female (measured in millimetres) at end of parturition.

Although the equation expresses the relationship between the size of the brood and the length of the female for domesticated grey guppies kept under the conditions described in this paper, fish which have received insufficient or unsuitable food have smaller broods in relation to their size. One fish, forty-millimetres long, which was bought from a pet shop and had a very emaciated appearance, had only eighteen fry in a brood and died shortly afterwards.

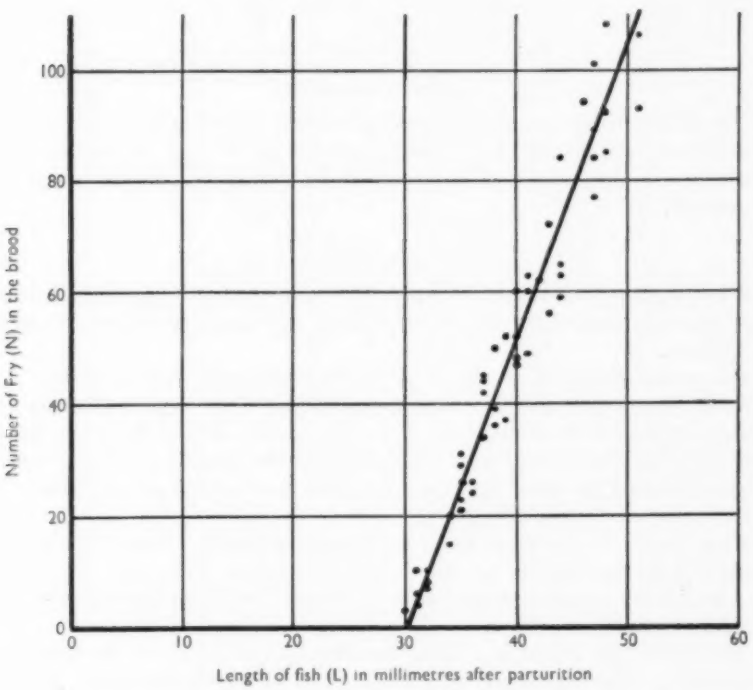

Fig. 3.—The size of broods in domesticated grey guppies.
$\mathbf{N}=5{\cdot}2\ \mathbf{L}-155\pm(0{\cdot}7\,\mathbf{L}-14)$.

The sizes of the first broods from the six larger fish are shown in Table 1. When these results were analysed it was found that the broods from the six larger fish and those from the two controls were also covered by the general formula.

It would appear that when no restriction to mating exists the first parturition occurs when the female is relatively small and the brood is small. If, however, mating is prevented until the female is larger then the first brood is larger but still conforms to the same linear function of the length at parturition.

TABLE 1

First broods from large guppies.

Total length of fish (mm.) after parturition	Number of fry in brood
33 (control)	16
34 (control)	19
42	63
43	69
43	60
44	79
44	66
48	93

ACKNOWLEDGMENTS

The author wishes to record his appreciation of the help given by Mr T. Horeman who constructed the maternity cages, Mr W. G. Phillips for valuable discussions on the culture of guppies and Dr James W. Atz for reading the manuscript.

SUMMARY

When a guppy is born the swim-bladder is not inflated, the specific gravity is greater than that of the water and when not swimming actively it sinks to the bottom.

The initial inflation of the swim-bladder normally occurs within a few seconds of birth when the fry swims to the surface of the water and gulps down a bubble of air which is forced along the pneumatic duct to the swim-bladder. Once the swim-bladder has been inflated the specific gravity of the fish approximates to that of the water and the fry is able to maintain any position off the bottom without a great effort.

From birth to the time when the swim-bladder is inflated fry are very vulnerable to cannibalism by the female parent and other fish.

A maternity cage is described which prevents the female fish from devouring fry at and after parturition.

The size of the brood is a linear function of the length of the female after parturition. The first brood may be large or small depending on the size of the female at the first parturition.

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NOTES AND ABSTRACTS

MEETINGS OF THE SOCIETY FOR SCIENTIFIC BUSINESS

11th October, 1960

SIR LANSBOROUGH THOMSON, C.B., O.B.E., M.A., D.Sc., LL.D.,
Vice-President, in the Chair

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE JUNE, JULY, AUGUST AND SEPTEMBER, 1960

BY L. HARRISON MATTHEWS, M.A., Sc.D., F.R.S.

The registered additions to the Zoological Society's Menagerie in London during the months of June, July, August and September were 542 in number. The following are of special interest :—Two female leopards *Panthera pardus* were presented by Mr A. I. Leetham and a male by Mr G. B. Eastmure. These three animals, which include a pair of the black variety, are from the same litter ; they were separated soon after birth and hand-reared by their donors. The black pair are exhibited together in the Lion House. The Earl of Cranbrook presented two serotine bats *Eptesicus serotinus* (Schreber) which are new to the collection. Other gifts include an angwantibo *Arctocebus calabaricus* from Mr J. C. Davidson, a male cheetah *Acinoyx jubatus* from Mr J. E. Sutton and four brown lemurs *Lemur fulvus*. The cheetah fills an important gap in the collection which has existed for the past two years. Four golden marmosets *Leontocebus rosalia*, three negro tamarins *Tamarin, tamarin*, a Baikal seal *Phoca sibirica*, a collection of kangaroos and wallabies and an echidna *Tachyglossus aculeatus*, have been received in exchange. The echidna was acquired as a mate for the specimen received in 1954. A white-headed two-toed sloth *Choloepus hoffmanni*, new to the collection, was purchased. Births included a Malayasian fruit bat *Cynopterus barchyotis*, and a female giraffe *Giraffa camelopardalis*. Birds new to the collection included a brown violet-eared humming bird *Colibri delphinae*, received in exchange, an Isthmian sugar bird *Cyanerpes caeruleus isthmicus* from Mr R. W. Drury, a chestnut-winged guan *Ortalis erythroptera* Sclater and Salvin from Mr T. Spence a Christmas Island frigate bird *Fregata andrewsi* Mathews from Captain D. Scorgie, two eastern pratincoles *Glareola maldivarum* J. R. Forster and two Ruppell's weavers *Ploceus galbula* Rüppell from Messrs G. H. and J. R. Newark. Three quetzals *Pharomacrus mocinno* were received in exchange, an Eritrean shikra *Astur badius sphenurus* was presented by Mr John Bowden C.M.Z.S. and two Abyssinian ground hornbills *Bucorvus abyssinicus* were purchased. A night heron *Nycticorax nycticorax* and two sarus cranes *Grus antigone* were hatched in the Menagerie. The two young

sarus cranes, hatched on the 17th July, are the first to be bred in the Gardens. The parents nested during 1958 and 1959 but the eggs proved infertile. The incubation period was thirty days and the chicks are now (at 12 weeks of age) almost two-thirds the size of the adults. Among the reptiles and amphibians new to the collection were a western serpentiform skink *Riopa anchietae*, five frogs *Pseudhymenochirus marlini* and a goliath frog *Rana goliath*. Other additions of interest were a grey monitor *Varanus griseus* presented by Mr K. Howard, two Pacific Coast hylas *Hyla regilla* presented by Lord Chaplin, two Storm's water cobras *Boulengerina annulata stormsi* presented by Mr C. J. P Ionides and a king cobra *Naja hannah* and an Indian cobra *Naja naja* presented by Mr N. C. Bucknall. Twenty ribbon snakes *Thamnophis sauritus* were born in the Menagerie. The Aquarium has received two interesting collections of marine animals from Madeira : these included octopus, flat lobsters, giant whelks and many other invertebrates as well as fishes. Other interesting additions to the invertebrate collection included a number of land hermit crabs from the Cocos Islands and land crabs from Trinidad. During the same period there were 365 additions to the Menagerie at Whipsnade Park, including some domestic animals and excluding transfers from London. The following are of special interest:—A nilgai *Boselaphus tragocamelus*, a great Indian rhinoceros *Rhinoceros unicornis*, a moose *Alces alces*, a Père David's deer *Elaphurus davidianus*, two snow leopards *Panthera uncia* and two muntjac *Muntiacus muntjac*, born in the Park. Three northern lynx *Felis lynx* were received in exchange from Zoo-centre Moscow ; two black rhinoceros *Rhinoceros bicornis* were purchased and two caracal lynx *Felis caracal* were presented by Nairobi National Park.

The following communications were read and discussed :—

Mr J. D. Macdonold. The secondary external nares of the gannet. [To be published in the " Proceedings "].

Professor D. M. S. Watson, F.R.S. The anomodont skeleton [To be published in the " Transactions "].

Dr L. Harrison Matthews, F.R.S. " Faune Cavernicole " [Film].

FOOD PREFERENCES OF THE GIRAFFE

By Anne Innis Dagg

Giraffe have definite preferences among the kinds of leaves that they eat, (Innis, 1958). It is reasonable to suppose that these preferences may be based on the chemical composition or the appearance of the leaves. Appearance does not seem to be important as giraffe browse freely at night.

This research project has been carried out to see if various chemical components of the leaves can be correlated with the giraffe's preferences. Twenty species of leaves were dried and collected in May, towards the end of the summer. At this time of the year all the trees and bushes are in full leaf and the giraffe have a wide selection of leaves from which to choose. The giraffe ate some of these species of leaves and ignored others. The leaves

were collected from the giraffe-inhabited Fleur de Lys Farm, Klaserie, in the Eastern Transvaal of South Africa.

The leaves have been partially analyzed and the results are tabulated in the Table. The analysis methods used were those outlined by W. Horwitz, (1955).

Partial analysis of South African dried leaves collected in May, 1957, from Fleur de Lys Farm, Klaserie.

Name of leaf	Giraffe preference 1*	Percentage on dry basis		
		Ash	Crude ether extract	Crude protein 2* 3*
Combretum imberbe	6	12·2	16·4	4·7
Pterocarpus angolensis	6	7·3	10·2	5·0
Cassia abbreviata	6	9·9	11·6	7·5
Ziziphus mucronata	5	12·4	7·8	3·5
Dalbergia melanoxylon	5	7·4	4·9	5·0
Strychnos dysophylla	5	11·9	7·2	4·4
Acacia nigrescens	5	10·2	8·2	5·6
Ficus petersii	4	18·4	6·8	4·3
Terminalia sericea	3	23·5	10·7	4·4
Acacia swazica	3	8·2	8·6	4·4
Combretum gueinzii	3	8·9	12·0	5·6
Sclerocarya caffra	2	14·8	6·9	4·7
Combretum transvaalense	1	12·4	9·1	6·6
Schotia brachypetala	0	19·5	8·5	—
Diospyros mespiliformis	0	11·6	13·8	8·4
Lonchocarpus capassa	0	11·4	10·1	5·0
Piliostigma thonningii	0	12·0	6·0	4·7
Pterocarpus rotundifolius	0	8·7	7·9	3·7
Ficus sp.	0	18·3	8·4	3·4
Cassia petersiana	0	9·2	11·2	5·3
Evergreen oak 4*	—	3·6	7·9	6·9

1*Key to giraffe preference : 0—none eaten ; 1—very little eaten ; 2—little eaten ; 3—some eaten ; 4—fairly well eaten ; 5—most eaten ; 6—all eaten within reach. Data is taken from the work of Innis, (1958).

2* The nitrogen content of the leaves has been estimated as 16 per cent of the protein content. (Pearsall, 1950).

3* The percentages of protein present in the leaves was generally lower than the percentages given by Bonsma (1942), possibly because of the poor rainfall in the summer of 1956–7 at Fleur de Lys Farm.

4* The evergreen oak leaves were collected in London from the supply fed to the giraffe at the London Zoo.

From this Table there is no evident correlation between the giraffe's preferences and the ash, crude ether extract and crude protein content. In accordance with this, Bonsma (1942) found that the protein content of mopani leaves (Copaifera mopane) was exceptionally high, but these leaves are not eaten by giraffe.

It has not yet been possible to do further work on the food preferences of giraffe. An analysis of the above leaves for steroid content and the presence of trace elements may yield more positive results.

Six sets of giraffe droppings collected at monthly intervals have been analysed for their crude fibre content. It may have been expected that a higher fibre content would be found in the droppings collected in the winter when food was scarce and the giraffe subsist largely on twigs, but there was no such correlation in the results.

I am grateful to Waterloo University for the use of their laboratory facilities.

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DELAYED BIRTH IN A HILL-KANGAROO, THE EURO, (*MACROPUS ROBUSTUS*)

By R. M. Sadleir and J. W. Shield

Zoology Department, University of Western Australia

Loss of a pouch joey, either by experimental procedure or by misadventure in the field, has been established in at least four macropod species (Sharman 1954, Sadleir & Shield 1960) as a sufficient, but not absolutely necessary, preliminary to the production of a second joey by the process of delayed implantation (Sharman, 1955). That premature loss of a joey is not absolutely necessary can be inferred from Carson's (1912) report of a case in the marloo (*Macropus rufus*) where a second joey appeared in the pouch after the initial joey had left the pouch spontaneously. In Carson's case the female had been segregated from males since early in the development of the initial joey Sharman (1955), working with the quokka (*Setonix brachyurus*), gave an account of the occurrence of a ' delayed ' joey following the spontaneous exit from the pouch, 171 days after birth, of the initial joey.

During the course of work on delayed implantation in the euro (*Macropus robustus*) we have recently found that a ' delayed ' joey may be produced after the initial joey has vacated the pouch. On the 28th July, 1959 a female euro was obtained which had been in captivity some months. Her pouch contained a 62 gram male joey. The joey was left in the pouch and from this date onward the famale was segregated from males. By the 29th January 1960 the joey had grown to 2.9 Kg and although still suckling had ceased to occupy the pouch. Further examination on 2nd March, 1960 showed an 11 gram joey in the pouch. It seems therefore that the marloo, the quokka and now the euro can produce a ' delayed ' joey after the normal exit from the pouch of the initial joey. Further work is being done on this phenomenon in the quokka and the euro.

We acknowledge financial assistance from Western Australian University Research Grants and a generous grant for marsupial research from the Commonwealth Scientific and Industrial Research Organisation.

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ERRATA

Vol. 135, Part 1

p. 138, line 4
p. 140, line 1
p. 142, line 19

for "groins" read "groynes"

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